Remarkable diversity of beetles (Coleoptera) in the late Triassic (Norian) "solite deposit" of Virginia and North Carolina

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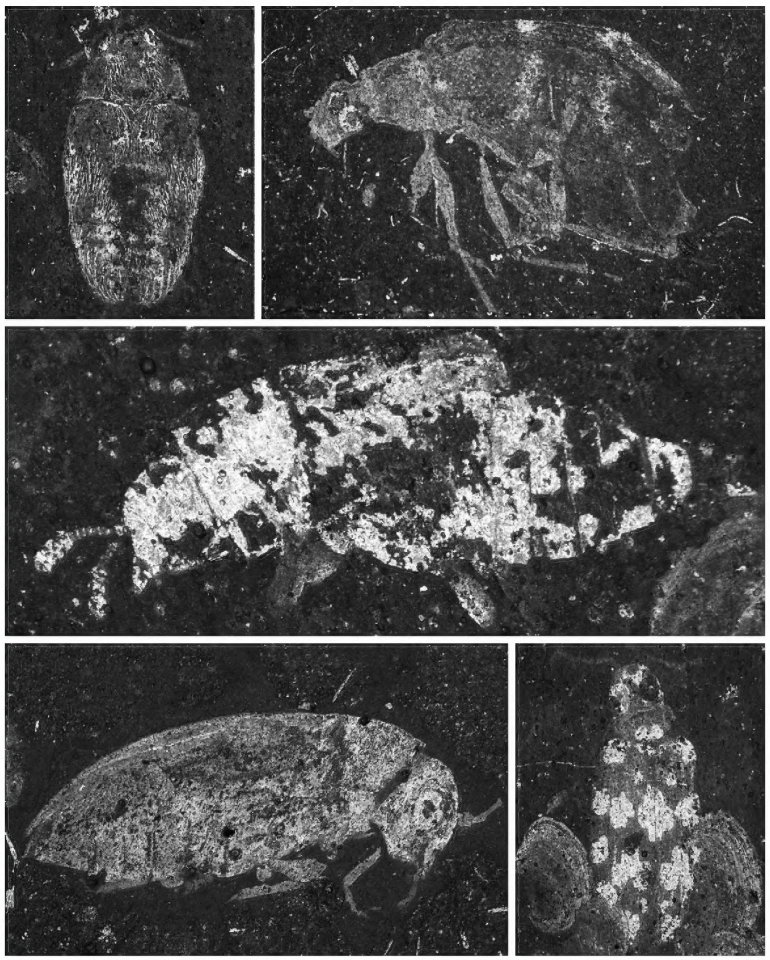

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REMARKABLE DIVERSITY OF BEETLES (COLEOPTERA) IN THE LATE TRIASSIC (NORIAN) "SOLITE DEPOSIT" OF VIRGINIA AND NORTH CAROLINA

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ABSTRACT

Known from over 50 Triassic localities worldwide, beetles were a significant component of the early Mesozoic paleofauna. Beetle fossils are particularly diverse in the Late Triassic (Norian) Cow Branch and Walnut Cove formations (Solite deposit) of Virginia and North Carolina, with 100 distinct morphotypes sorted from approximately 1000 specimens. The diversity of the Solite Coleoptera is documented, the 100 beetle morphotypes are informally described, and comparisons are made with other beetle communities through geologic time. In comparison with modern beetle communities, the Solite fauna shares two remarkable similarities. First, the distribution of Solite beetle body sizes matches that of some modern beetle communities, with the majority of specimens in both groups measuring between 2 and 4 mm in length. Second, the vast majority of the 100 Solite morphotypes (84%) are known from only a single specimen. This pattern somewhat follows the species abundance distribution of modern animal communities, in which a community is comprised of only a few common species and many rare species. In contrast, the Solite beetle fauna differs markedly from those of other Triassic and Early Jurassic deposits, both in the composition of higher taxa present, as well as in the lack of shared taxa between sites. The uniqueness of the Solite taxa, including the remarkable diversity, demonstrate the importance of the Solite Konservat-Lagerstätte in understanding the evolutionary history of Order Coleoptera.

INTRODUCTION

With over 380,000 described species, Coleoptera is the most speciose order of animals today (Ślipiński et al., 2011). Varying immensely in morphology, beetles are both some of the smallest as well as some of the largest insects alive, ranging from the <1 mm featherwing beetles (Ptiliidae) to the 190 mm Hercules beetles (*Dynastes*: Scarabaeidae). Intertwined with their morphological diversity, beetles inhabit nearly every terrestrial environment, in addition to many aquatic ones. They are also among the most common insects preserved in the fossil record, owing to their durable, hardened elytra (forewings).

While some molecular models predict a Carboniferous origin for Coleoptera (Toussaint et al., 2017; Zhang et al., 2018; McKenna et al., 2019; Cai et al., 2022), the earliest definitive fossil beetle, *Coleopsis archaica*, is not known until the early Permian (~295 Ma; Kirejtshuk et al., 2014; Schädel et al., 2022). During the Permian, the beetle fauna consisted of the early stem groups Tshekardocoleidae and Permocupedidae, as well as members of suborder Archostemata, but their diversity and abundance remained relatively low (Zhao et al., 2021). The first members of suborder Adephaga appear in the fossil record in the latest Permian; Myxophaga and Polyphaga most likely appeared before the end of the Permian, but definitive fossils of these groups have not yet been found from this time (Zhao et al., 2021; Beutel et al., 2024).

The Permian ended with the greatest mass extinction of the Phanerozoic, most often attributed to the eruption of the Siberian flood basalts (Saunders and Reichow, 2009), an event that led to the restructuring of many habitats. While Permian stem-group beetles did not survive into the Mesozoic, many extant insect families first began to increase in abundance during the Triassic. The fossil record of the Early Triassic is poorly known for insects in general, with only a small number of beetle remains (almost exclusively isolated elytra) having been collected from this period (Ponomarenko, 2016a). It was not until the Middle Triassic that beetle taxonomic diversity recovered; while Archostemata was still well represented, beetle assemblages became dominated by new taxa (e.g., Cupedidae, Phoroschizidae; Zhao et al., 2021).

Coleopteran fossils have been reported from over 50 Triassic deposits on every continent including Antarctica, but only a few of these have produced prolific insects (fig. 1). Beetles are generally abundant in all of the major Triassic insect deposits including the Madygen For-

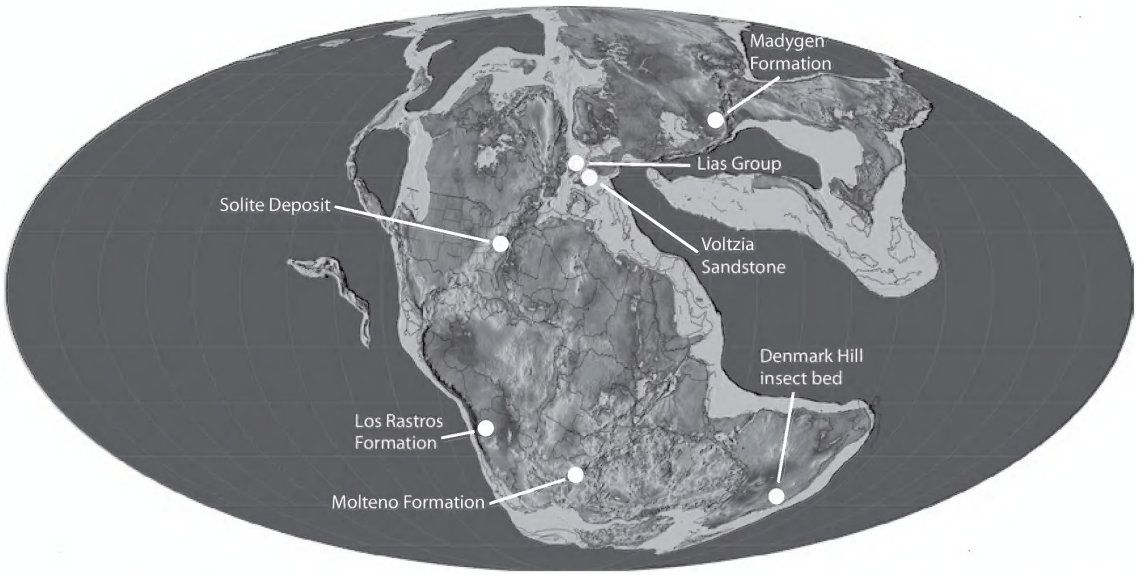


FIG. 1. Paleogeographic map showing the approximate locations of the major Triassic insect deposits preserving beetles. Modified from Carnian Map #45 of the PALEOMAP Project (Scotese, 2014).

mation of Kyrgyzstan, the Molteno Formation of South Africa, the Los Rastros Formation of Argentina, and the Denmark Hill insect bed of Australia. Perhaps less well known, the Solite Konservat-Lagerstätte of Virginia and North Carolina is another prolific Triassic insect deposit preserving one of the earliest-known post-Permian extinction assemblages of both terrestrial and freshwater insects. While not quite as abundant as in the other major deposits, the Solite beetles are remarkably diverse, with at least 100 distinct morphotypes.

Locality and Materials

The Solite insects are preserved as two-dimensional, silvery carbon films in a matrix of fine-grained, black mudstone. Most specimens are very small (generally <4 mm in length), and many are fully articulated with microscopic details like microtrichia often preserved. The Solite insects come from two separate geologic formations: the Cow Branch Formation and the Walnut Cove Formation. Herein, the fossiliferous portions of these two formations are referred to as the "Solite deposit." This deposit is located in the Dan River Basin, one of the continental rift basins of the Newark Supergroup throughout the northeastern United States that spans southern Virginia and northern North Carolina (Olsen et al., 2015).

The Cow Branch Formation outcrops in the former Solite Corporation Quarry, located on the Virginia-North Carolina border at Cascade, Virginia (approximately 36° 32′ 29.7″ N, 79° 40′ 12.8″ W). The quarry is composed of three separate pits, designated A, B, and C by Fraser and Grimaldi (2003: fig. 1b). The majority of the insects here come from the aptly named "insect layer" (cycle 2; Olsen, 1979), a 34 mm thick unit outcropping in pit B that has been systematically excavated. The fossils from this pit are roughly 220 million years old (Norian; Olsen et al., 2015; Kent et al., 2017). Though fewer in number, some insects have also been recovered from the slightly older sediments of pit C (ca. 221 Ma). The remaining Solite insects come from the poorly studied Walnut Cove Formation, formerly referred to as the Lower Cow Branch Formation (see Olsen et al., 2015). It outcrops in Madison, North Carolina (approximately 36° 23′ 13.8″ N, 79° 56′ 15.6″ W), about 30 km southwest of the Solite Quarry. The magnetostratigraphy of this

unit is unresolved, but its age is roughly estimated to be between 227.5 and 224.5 million years old (Olsen et al., 2015: fig. 5).

The Cow Branch Formation consists of repeating cycles of microlaminated mudstones and massive, mudcracked sandstones that preserve Van Houten cyclicity. Olsen et al. (1978) suggested that these layers were deposited in a deep, perennially stratified lake. The small area of the lake (as compared with its depth) would prevent the occurrence of wind mixing and thus oxygen from reaching the lake bottom. This lack of oxygen would have prevented both decay and bioturbation, allowing fully articulated insects to preserve. Liutkus et al. (2010) challenged this interpretation, positing that the geochemistry of the insect layer suggests a shallow, saline, and alkaline lake. The abundance of conchostracans, which often inhabit brackish environments, in addition to the assortment of insects preserved, specifically the near lack of aquatic insect nymphs that respire via tracheal gills (e.g., Ephemeroptera, Odonata, Plecoptera), also support the notion of unusual water chemistry (see Fraser et al., 2017, for a discussion of this topic). However, it should be noted that the Solite sediments have been metamorphosed, as evidenced by the hardness of the rocks, their parallel bedding planes, and the lack of relief preserved in the Cow Branch fossils. Exposure to high temperatures and pressures during the process of metamorphism would likely have altered the original geochemical signatures of the rock, bringing their reliability into question. Additionally, there is one somewhat common arthropod in the Solite material that possesses a set of apical structures that appear to be gills. This organism was originally described as a possible phyllocarid crustacean (Olsen et al., 1978), but its identity remains in question. Regardless, the presence of apparent gills suggests that at least some organisms were obtaining oxygen directly from the water.

The lithology of the Walnut Cove Formation is very similar to that of the Cow Branch, with the exception of a rooted mudstone facies sometimes overlain by thin coal beds (suggesting a swamp environment) and, more importantly, the lack of microlaminated beds (Olsen et al., 2015). The rocks of the Walnut Cove Formation are also much more pristine (e.g., crumble easily, often with orange-colored weathered patches) than the low-grade metamorphic sediments of the Cow Branch Formation (Heckert et al., 2012: appendix), indicating slightly different geologic histories and possibly depositional environments. In contrast to the Cow Branch insects, those of the Walnut Cove Formation are almost exclusively fragmentary, as is more common of Triassic insect deposits worldwide.

The Solite insect collection comprises roughly 9400 specimens, with at least nine orders known from this deposit (Fraser et al., 2017). While beetles are not the most abundant insects at Solite, they are certainly the most diverse. Comprising approximately 19% of identifiable specimens, there are at least 100 distinct morphotypes present. The goal of this paper is therefore to document the diversity of the Solite Coleoptera and compare the fauna preserved here to other major entomofaunas of the Early Mesozoic.

Methods

Beetle specimens were wetted with 70% ethanol to increase contrast between the fossilized carbon film and mudstone matrix. Specimens were viewed using a Nikon SMZ1500 stereomicroscope fitted with a fiber optic ring light, which provided a nondirectional, diffuse light source necessary for illumination of the silvery film by which the insects are preserved. For optimal observation of elytral striae, which are sometimes faint, fossils were viewed tilted at an angle while dry to accentuate the slight relief (fig. 2). Articulated specimens were sorted into morphotypes based on size, body proportions, and details of the elytra, including shape, pattern, and microsculpture. The best-preserved specimen of each morphotype was photographed using a Nikon 16MP camera and Nikon Elements NIS software, illustrated using Adobe Illustrator, and informally described. Isolated elytra were also

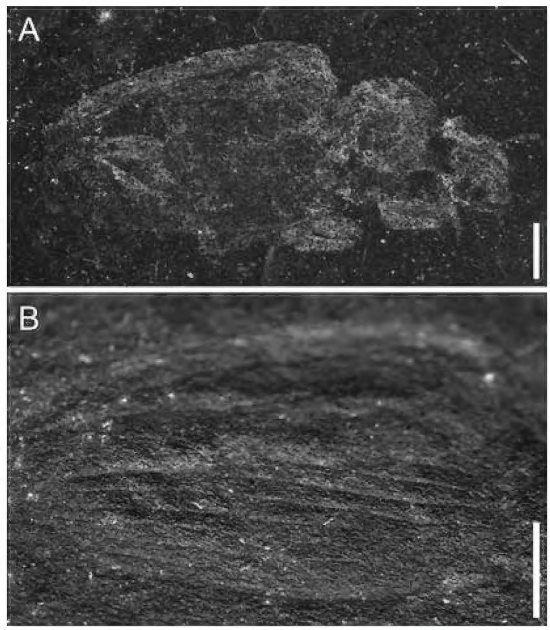


FIG. 2. Comparison of specimen viewing methods. **A.** Solite specimen YPM IP 388741 (morphotype 46) under alcohol. Note that elytral striae are not visible. **B.** Same specimen dry and tilted showing slight relief of striae. Scale bars: 1 mm.

sorted into separate elytral morphotypes based on size, proportions, patterns, and microsculpture; the best preserved of each was photographed, illustrated, and informally described. All distinct elytra with fair to excellent preservation were included; fragmentary specimens or those with very poor preservation were omitted. All specimen measurements were taken using ImageJ software. For articulated specimens, length was measured from the most anterior part of the body (usually the anterior margin of the head, excluding appendages) to the tip of the abdomen or elytra (excluding any terminalia). Width was measured at the widest point, usually across the middle of the elytra. For isolated elytron specimens, measurements were taken at the longest and widest points.

Abbreviations

The majority of the specimens examined in this study are housed at the Virginia Museum of Natural History (VMNH) in Martinsville, Virginia. The remaining specimens are housed at the American Museum of Natural History (AMNH) in New York, and the Yale Peabody Museum of Natural History (YPMNH) in New Haven, Connecticut.

The Solite Beetles

The Solite insect collections contain roughly 1080 beetle specimens, which are almost evenly split between the Cow Branch and Walnut Cove formations. Many beetles from the Cow Branch Formation are fully articulated while those of the Walnut Cove Formation are almost exclusively represented by isolated elytra. The Walnut Cove specimens are also more friable, but have greater relief. To understand the beetle diversity in this deposit, each unique morphotype was illustrated and informally described. Where possible, assignment to taxonomic rank below order is discussed. Classification of modern beetles is often based on antennal, mandibular, coxal, and tarsal structure, features that are not often pre-

served in lithified fossils. The two-dimensional and frequently dorsal preservation of the Solite specimens makes further classification especially difficult. Thus, with the exception of two previously described species (*Leehermania prorova* Chatzimanolis et al., 2012 [Myxophaga] and *Holcoptera solitensis* Thomson et al., 2017 [Adephaga: Coptoclavidae]), the specimens herein are referred to as morphotypes and have not been assigned to families, genera, or species. In total, 100 distinct morphologies are known from the Solite beetle fauna: 61 morphotypes from the articulated material, 37 morphotypes from the isolated elytra, and the two previously described species, *L. prorova* and *H. solitensis*. Because the morphologies of the isolated elytron specimens generally differ from those of the articulated specimens, there is little overlap between the two groups of morphotypes. In the few instances where an isolated elytron was similar to that of an articulated specimen, this was noted in the respective morphotype descriptions.

Articulated Specimens: Including the already published *Leehermania prorova* (Chatzimanolis et al., 2012) and *Holcoptera solitensis* (Thomson et al., 2017), there are 63 morphotypes of articulated beetles from the Solite deposit. Additional specimens exist, possibly belonging to unique morphotypes, but their preservation was too poor for examination and comparison. The articulated morphotypes discussed herein generally have the head, pronotum, and both elytra preserved; occasionally parts of the legs, antennae, and palps are also visible. Additionally, the majority of the Solite specimens are preserved in a dorsal view. All articulated morphotypes are from the younger Cow Branch Formation; only two articulated specimens were found in the Walnut Cove material, but the preservation of the first was too fragmentary to examine, and the second was similar in habitus to Solite morphotype 16 (fig. 18) from the Cow Branch Formation.

Specimens range in length from 1.6 mm to over 33 mm (fig. 3). Of the morphotypes where length is measurable, the vast majority (84%) are less than 6 mm long (mean 4.5 mm, median 3.8 mm). The remaining nine morphotypes range from 6.9 mm to 12.7 mm. Because many Solite beetles are preserved only as isolated elytra, examination of the elytra of the articulated specimens is necessary for comparison between the two assemblages. Elytra of the articulated beetles range in length from 0.8 mm to 8 mm (mean 3 mm, median 2.6 mm), with the majority of measurable specimens (81%) being less than 4 mm in length. One additional specimen (morphotype 61, figs. 66, 67) is greater than 33 mm in body length (elytra >21 mm in length, missing the apical portion) and is a clear outlier among the Solite beetles.

There exists a wide variety of elytral microsculpture, patterning, and vestiture among the Solite beetles (fig. 4; table 1). Microsculpture refers to small structural features of relief of the cuticle, such as striae, nodules, punctures, and window punctures. Vestiture refers to hairlike structures including setae, setulae, and microtrichia. Patterning refers to the color patterns present on some of the Solite elytra and may be caused by differing cuticular melanin contents (Wang et al., 2023).

Of the 59 morphotypes preserved with the details of their elytra visible (i.e., preserved dorsally or laterally), the majority are smooth and lacking in microsculpture (N = 33, 56%); seven of these have distinct color patterns. A smaller number (N = 20, 34%) are striate (one with a distinct color pattern), four are punctate (7%), and only two (3%) are covered in dense nodules (table 2). Specimens with smooth elytra have the greatest range in total body length (1.6–12 mm; elytra 1.2–8 mm). Striate specimens are a bit smaller, ranging from 2.2 mm to 8.5 mm in body length (elytron length 1.6–5.4 mm) and the four specimens with punctate elytra are larger (5.9–12.7 mm in body length; elytra 4.5–7.7 mm in length). The single very large specimen measuring over 33 mm in length (morphotype 61, figs. 66, 67) possesses nodular elytra, as does a second much smaller specimen, morphotype 35 (fig. 40), measuring 5.2 mm.

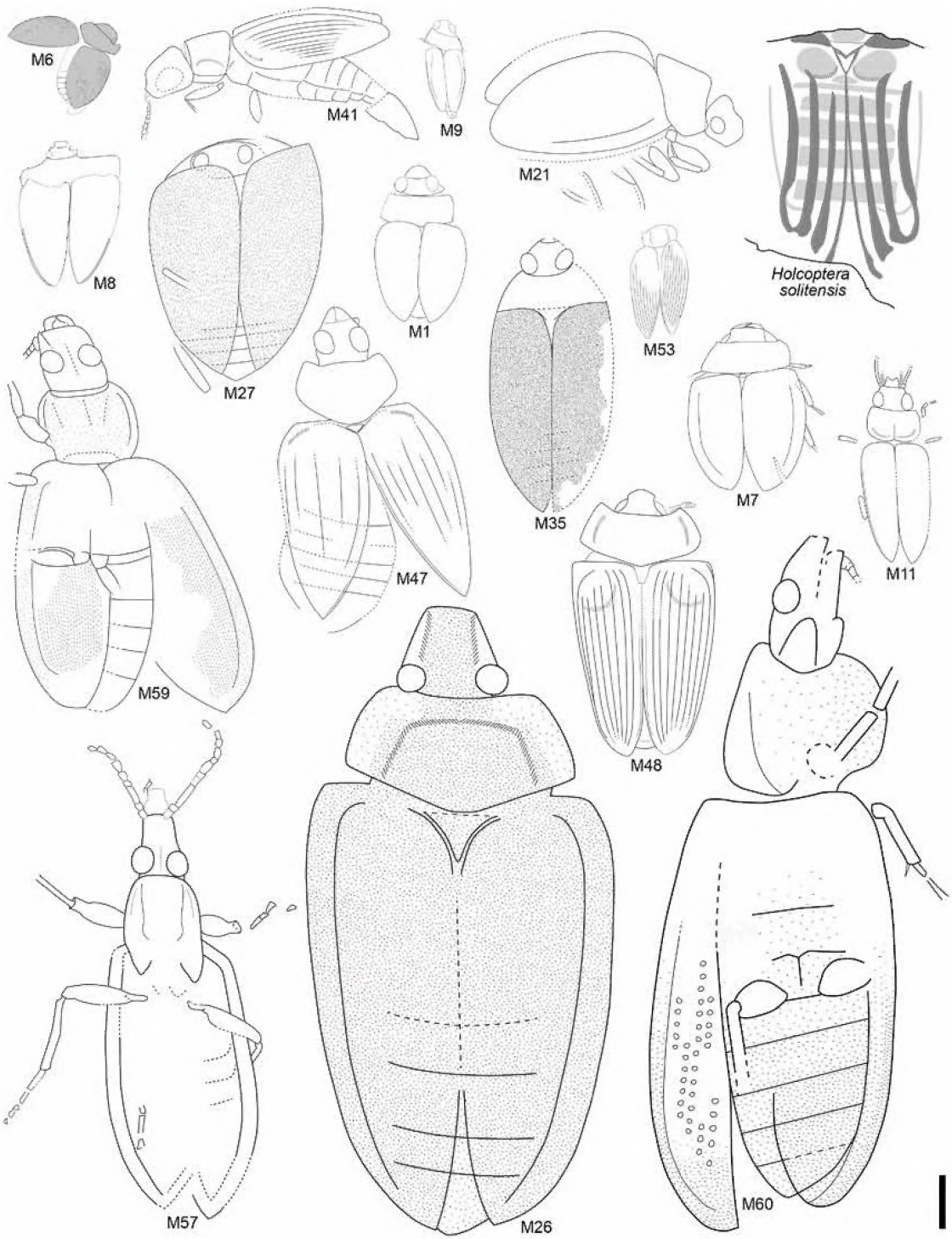
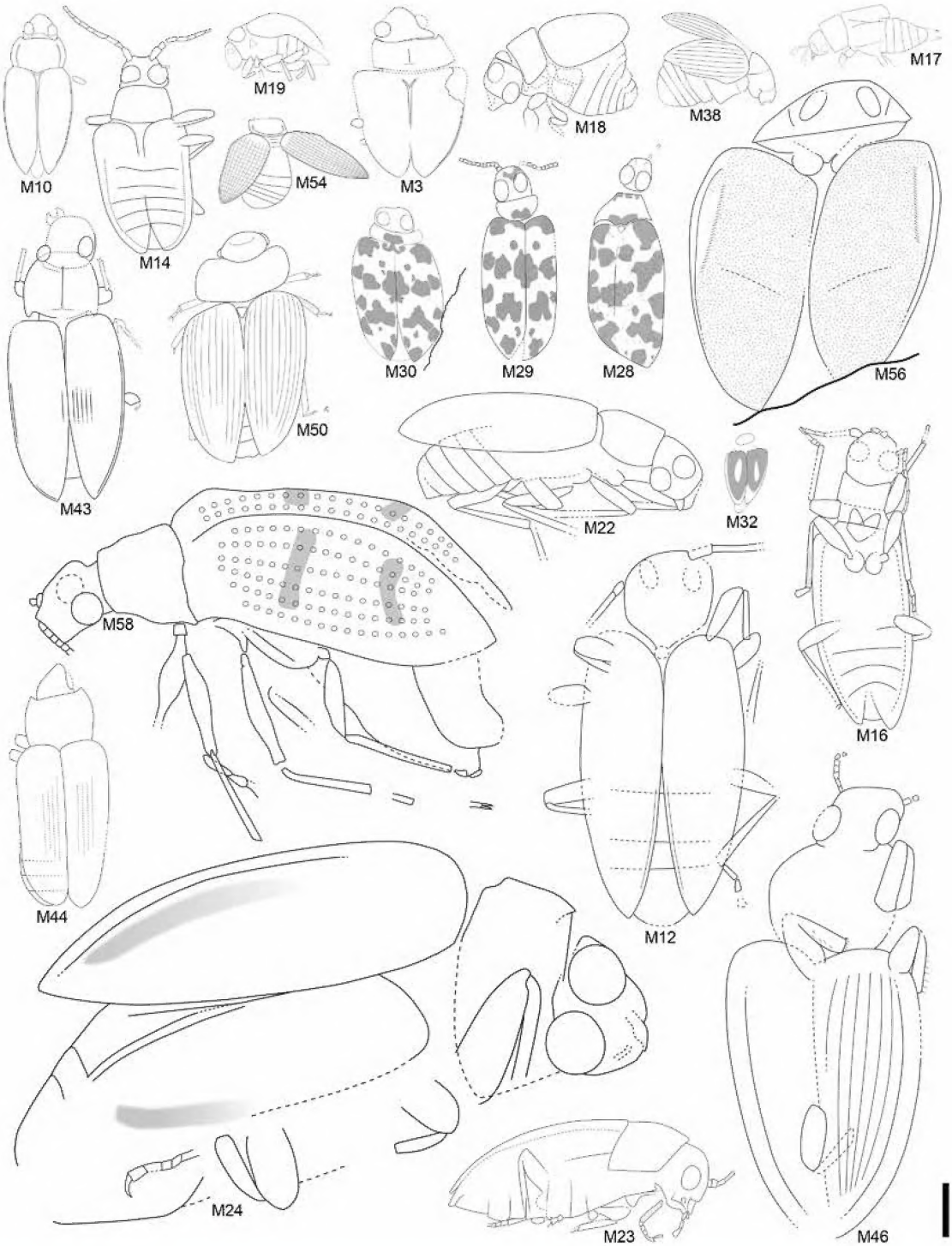


FIG. 3. Diversity of the articulated Solite beetles (*above and opposite page*). Specimens are drawn to the same scale. M# near each panel is the morphotype number; the largest, M61, is omitted. Scale bar: 1 mm.


M10
M19
M14
M54
M3
M18
M38
M17
M56
M30
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M46

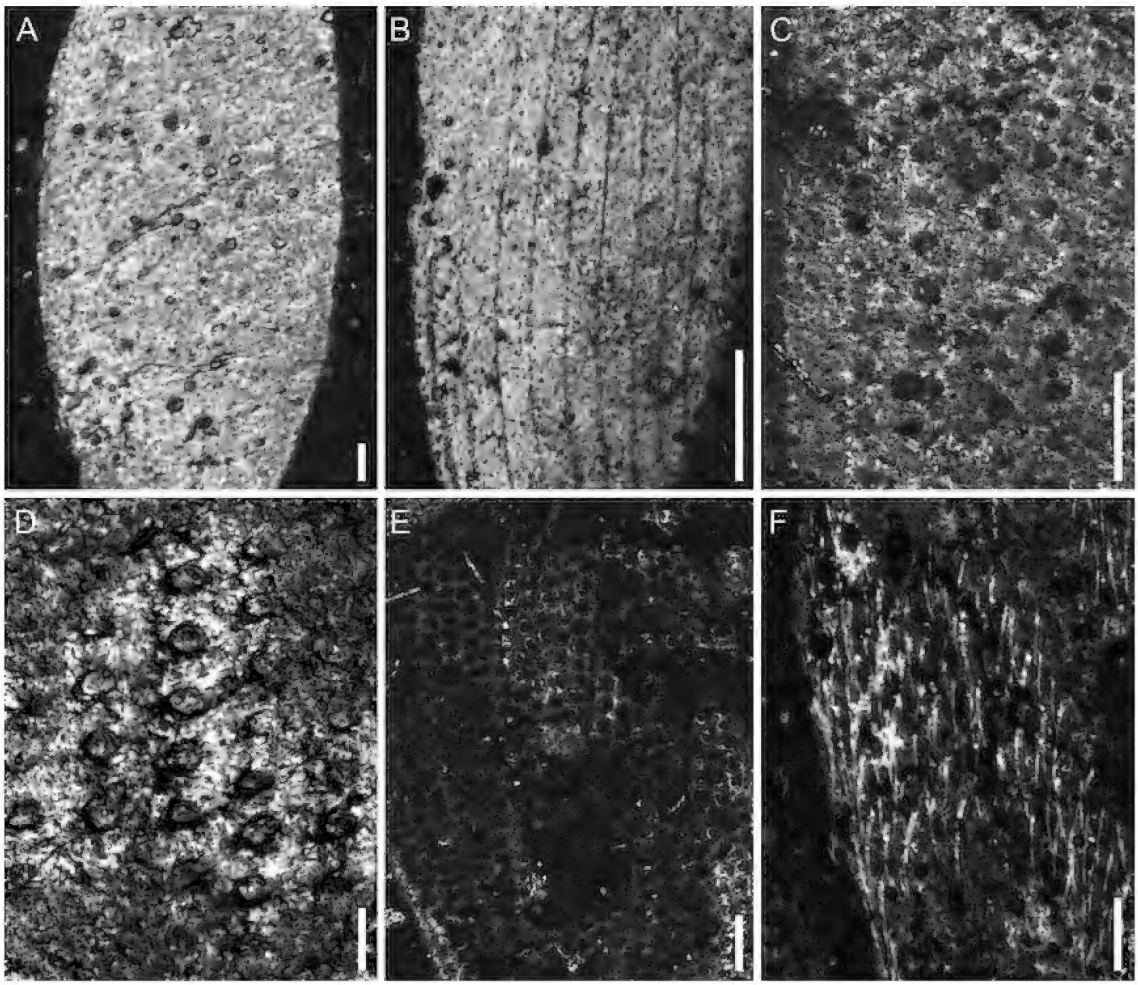

FIG. 4. Examples of elytral microsculpture and vestiture found in the Solite beetles. **A.** Smooth, morphotype 63. **B.** Striate, morphotype 90. **C.** Punctate, morphotype 76. **D.** Nodules, morphotype 70. **E.** Window punctures, morphotype 73. **F.** Setae, morphotype 31. Scale bars: A, D, F: 0.1 mm; B, C, E: 0.5 mm.

Isolated Elytra: Though isolated elytra do not possess sufficient diagnostic features for taxonomic classification, they are still useful for distinguishing beetle morphotypes. Some authors have used formal taxa to organize isolated elytra; we have chosen instead to organize the Solite deposit's isolated elytra into elytral morphotypes in a similar way to that used for the articulated specimens. In this study, 37 elytral morphotypes have been separated: 29 from the Walnut Cove Formation and 8 from the Cow Branch Formation.

Because of the lower preservation quality of the Walnut Cove fossils, many of the isolated elytral specimens are fragmentary. Of the 37 elytral morphotypes, length is measurable in 24 and ranges from 1.6 mm to 15 mm (mean 3.7 mm, median 2.9 mm; table 2). Additionally, larger elytra tend to be more fragmentary than smaller ones, with seven of the 13 remaining fragmentary morphotypes greater than 5 mm in length. Nineteen (51%) of the elytral morphotypes are striate, six (16%) are punctate, three (8%) are covered in distinct nodules, two (6%) have win-

TABLE 1

Elytral Terminology

Definitions of the microsculpture and vestiture types used to describe Solite beetle elytra.

	Term	Definition
Microsculpture	Striae	Long, narrow, parallel grooves in the cuticle; striate (adj.)
	Nodules	Convex, pimplelike structures on the cuticle; nodular (adj.)
	Punctures	Small pits or depressions in the cuticle, often rounded or circular; punctate (adj.)
	Window punctures	Large, square punctures. In living archostematans with incompletely sclerotized elytra, these are the "cells" between the longitudinal veins and crossveins.
Vestiture	Setae	Hairlike bristles with sockets
	Setulae	Tiny, fine setae with sockets
	Microtrichia	Microscopic, hairlike outgrowths of the cuticle; do not have sockets

dow punctures, and the remaining seven (19%) are smooth. Striate specimens make up the majority of the elytral morphotypes and range in length from 2.3 mm to over 7.5 mm. Morphotypes with punctures, as well as those with window punctures, tend to be larger and more fragmentary with only three of the eight total morphotypes fully preserved; they range in length from >5.6 mm to 15 mm. The three nodular specimens vary greatly in morphology; two are small (3.3 mm and 3.6 mm), and the other is >8.6 mm in length. The smooth elytral morphotypes are generally smaller than the others, ranging from 1.6 mm to 4.1 mm in length and are all fully preserved. Additionally, a few elytral specimens appear to have tubular veins along their margins. These veins are only present in specimens from the Walnut Cove Formation, which could be due to the more three-dimensional preservation of the specimens, or perhaps due a difference in the taxa preserved, which are estimated to be a few million years older than those of the Cow Branch Formation.

Morphotype and Species Accounts

The terms "part" and "counterpart" are used informally to denote whether both halves of the fossil have been recovered. Each description is accompanied by a plate containing photomicrograph(s) of the morphotype and an illustration. For each illustration, solid lines denote preserved, discrete boundaries of body parts or striae; dotted lines denote indistinct boundaries, areas that were not preserved, or overlapping body parts. The illustration and the first photomicrograph of each plate share the scale bar located between them, unless otherwise noted. Many plates also include additional photomicrographs of the counterpart (when present), morphological details of the specimen, and/or specimens sharing a similar morphology.

Articulated Morphotype Accounts

Morphotype 1

Figure 5A, B

Description: Small beetle (2.9 mm long, 1.7 mm wide) preserved in dorsal view; preservation fair; part and counterpart. Head, pronotum, and elytra preserved. Head with broadly convex anterior margin, clypeal suture distinct; eyes large, located laterally. Pronotum rectangular, width ~2.3× length, anterior and posterior margins parallel, anterolateral corners rounded, posterolateral corners right-angled. Elytra smooth, length ~2.1× width; anterior margins roughly

TABLE 2

Elytral Microstructure and Size

Numbers and lengths of articulated and elytral morphotypes possessing each type of microsculpture. Specimens for which length is not fully measurable are omitted from the total length size ranges.

	Articulated Morphotypes (no.)	Total Length (mm)	Elytron Length (mm)	Elytral Morphotypes (no.)	Elytron Length (mm)
Smooth	33	1.6–12	0.8–8	7	1.6–4.1
Striate	20	2.2–8.5	1.6–5.4	19	2.3 to >7.5
Punctate	4	5.9–12.7	4.5–7.7	6	>5.6–15
Nodular	2	5.2; >33	2.3; >21	3	3.3 to >8.6
Window Punctures	0	—	—	2	>6.4; >7.6
Elytral details not visible	4	4.5–7.8	1.8–3.6	—	—

straight, sutural margins slightly convex, apices pointed; no lateral rim evident. Abdomen tip visible between elytral apices.

Material: Single specimen, VMNH 95900.

Comments: Specimen not identifiable beyond order; somewhat similar in size and proportions to Cow Branch specimens VMNH 51302 and VMNH 95126, though poor preservation and generic shape preclude detailed comparisons.

Morphotype 2

Figure 5C, D

Description: Small beetle (3.4 mm long, 1.8 mm wide) preserved in dorsal view; preservation fair; no counterpart. Head, pronotum, and elytra preserved. Head with concave anterior margin; eyes large, located laterally. Pronotum somewhat rectangular, width ~2.8× length, anterior and posterior margins roughly straight and parallel; anterolateral corners minutely pointed, posterolateral corners rounded. Scutellum large, triangular; anterior margin indistinct. Elytra preservation coarse, apparently smooth, lacking microsculpture and setae; length ~2.6× width; anterior margins convex, sutural margins straight; apices bluntly pointed; thin lateral rim evident. Abdomen tip visible between elytral apices.

Material: Single specimen, YPM IP 036448.

Comments: Specimen not identifiable beyond order; similar to Cow Branch specimen YPM IP 388870, though differences in pronotum shape indicate separate morphotypes.

Morphotype 3

Figure 6A, B

Description: Small specimen (3.1 mm long, 2 mm wide) preserved in dorsal view; preservation fair; part and counterpart. Head, pronotum, possible minute fragments of leg, and elytra preserved. Head with slightly expanded preorbital area, anterior margin convex. Eyes apparently widely separated; left eye well preserved, right eye indistinct. Pronotum roughly rectangular, width 2.5× length, anterolateral corners pointed; median line distinct. Partial scutellum visible, apex pointed. Elytra smooth, length roughly 2× width, widest at basal margin and tapering apically; anterior and sutural margins straight; anterolateral corners rounded, thin lateral rim visible on right elytron; apices dully pointed. Two fragments visible on left side of body, likely part of the legs.

Material: Single specimen, AMNH 04-93.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 4

Figure 6C, D

Description: Small beetle (4 mm long, ~2.7 mm wide, estimated with elytra closed) preserved in a dorsal, slightly oblique view; preservation good; no counterpart. Head, pronotum, scutellum, three partial legs, both elytra, and faint portion of abdomen preserved. Eyes and anterior margin of head indistinct. Pronotum wide, fairly short, with small, slightly pointed anterolateral and posterolateral corners. Scutellum somewhat distorted, roughly triangular in shape with rounded corners. Three partial legs preserved: two left legs with thick femora and slender, elongate tibiae (width ~0.3× that of femur), lower leg with two tarsi and two tarsal claws visible; right leg poorly preserved with only partial femur and tibia. Elytra smooth, wider at anterior end, tapering slightly to a widely rounded point at apex; sutural margin straight; thin, lateral rim possibly present; elytra spread, showing poorly preserved abdomen beneath. At least four abdominal segments visible, lateral margins unclear.

Material: Single specimen, VMNH 129480.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 5

Figure 7A–E

Description: Small specimen (3.2 mm long) preserved in dorsal view; preservation good; part and counterpart. Head, pronotum, elytra, and abdomen preserved. Body ovate. Anterior portion of head triangular, clypeal suture faint; eyes large, laterally located. Pronotum preserved asymmetrically, somewhat pentagonal in shape; anterior margin strongly concave, posterior margin pointed medially, anterolateral corners pointed, posterolateral corners rounded. Elytra smooth, preserved with substantial relief; length 1.9× width, anterior margins roughly straight, sutural margins convex, apices sharply pointed; preservation too coarse for observation of setulae or microsculpture. Abdomen preserved between spread elytra, four tergites visible.

Material: Illustration and description based on VMNH 95086. Three additional specimens possibly belonging to this morphotype: VMNH 51275, VMNH 94862, and YPM IP 034686.

Comments: Specimen not identifiable beyond order; however, overall proportions and pronotum shape resemble those of *Phoroschizus* (= *Schizophorus*; Bouchard and Bosquet, 2020) *crassus* from the Jurassic of Kazakhstan (Ponomarenko, 1968). Body shape also somewhat common in the Solite deposit: similar to three other articulated specimens as well as isolated elytron morphotype 64 (fig. 68E, F).

Morphotype 6

Figure 8A–D

Description: Small beetle (1.6 mm long) preserved in a dorsal, somewhat oblique view with some relief; preservation excellent; part and counterpart. Head, pronotum, elytra, abdomen, and possible hind-wing tip preserved. Body surface heavily sclerotized. Head partially recessed beneath pronotum, anterior margin broadly rounded; eyes indistinct. Pronotum with straight anterior margin, anterolateral corner slightly projecting forward; posterior margin pointed medially. Elytra appear strongly convex; smooth, heavily sclerotized, covered in fine setae; length roughly 1.6× width; basal margins straight, sutural margins convex, apices sharply pointed; thin rim along lateral margins. Abdomen visible between spread elytra, six subequal segments preserved. Possible tip of hind wing extended past elytral apex.

Material: Single specimen, VMNH 53853.

COMMENTS: Specimen bears a resemblance to the basal polyphagan family, Clambidae; does not resemble any other beetle from the Solite deposit.

Morphotype 7

Figure 9A–D

DESCRIPTION: Small specimen (3.2 mm long, 2.2 mm wide) preserved in dorsal view; preservation good; part and counterpart. Head with eyes, pronotum, four partial legs, and elytra preserved. Body short, ovate. Head short, length 0.25× width; frontoclypeal suture straight; eyes large, laterally located, partially hidden by prothorax. Pronotum somewhat trapezoidal, length 2.8× width, anterior and posterior margins roughly straight and transverse; anterolateral corners small, pointed; posterolateral corners rounded. Small scutellum visible, ovate. One leg fragment on left side of body; three partial legs on right side: all with partial tibiae and tarsi; hind tibia with very short fringe of setae along margin. Elytra smooth, length roughly 2× the width; basal margins straight, apices rounded; wide epipleural rim present. Abdomen not preserved.

MATERIAL: Single specimen, VMNH 90298.

COMMENTS: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 8

Figure 10A–E

DESCRIPTION: Small beetle (2.8 mm long, 1.9 mm wide) preserved in dorsal view; preservation fair; part and counterpart. Head, partial pronotum, and partial elytra preserved with little detail. Body shape somewhat resembling that of Pentatomidae (Hemiptera: Heteroptera). Head with flat anterior margin and small, widely separated eyes. Pronotum much wider than head, anterior margin wide, fairly straight, with rounded anterior corners; posterior margin not preserved. Elytra smooth, entirely lacking microsculpture and vestiture; anterior portion subequal in width to pronotum; anterior margins not preserved, sutural margins straight, lateral rim thin, apices gently pointed.

MATERIAL: Single specimen, AMNH 04-90.

COMMENTS: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 9

Figure 11A–D

DESCRIPTION: Small specimen (1.7 mm long excluding terminalia, 0.7 mm wide) preserved in dorsal view; preservation good; no counterpart. Head, pronotum, one partial leg, both elytra, and terminalia preserved. Body elongate, somewhat streamlined, fusiform. Head with pointed anterior margin; eyes large, widely separated. Pronotum entirely smooth, anterior margin concave, thin lateral rim; antero- and posterolateral corners pointed. Scutellum small, triangular. Elytra entirely smooth, length 4× width, narrowing apically; anterior margins convex, sutural margins straight, apices rounded; lateral rim thin; a shallow shelf or furrow near outer margin of each elytron. Abdomen tip preserved showing partial genitalia; specimen appears to be male.

MATERIAL: Single specimen, AMNH 04-77.

COMMENTS: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 10

Figure 12A, B

DESCRIPTION: Small beetle (3 mm long, 1.2 mm wide) preserved in dorsal view; preservation good; no counterpart. Head, pronotum, one small leg fragment, elytra, and possible abdomen tip preserved. Body somewhat streamlined, faintly fusiform. Head large, anterior margin strongly convex and bluntly pointed, curved lobe or fold near posterior margin; eyes widely separated. Pronotum width approxi-

mately 1.5× length, lateral margins convex, anterolateral corners pointed; disc raised in center. Faint trace of small, rounded scutellum. One small leg fragment visible on right side of body. Elytra smooth, entirely lacking microsculpture and vestiture, length 3.3× width, sutural margins straight, apices pointed; very thin lateral rim. Possible trace of terminal abdominal segment visible between elytra.

Material: Single specimen, AMNH 04-88.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 11

Figure 13A, B

Description: Small specimen (3.5 mm long, 1.3 mm wide) preserved in dorsal view; preservation good; no counterpart. Head with antennae and mouthparts, pronotum, leg fragments, and elytra preserved. Head rectangular, length 0.7× width; eyes large, widely separated; labrum visible, anterior margin strongly concave; palp and antennal segmentation obscure. Pronotum somewhat rectangular, length 0.6× width, medial sulcus well defined posteriorly; anterior margin slightly concave; posterior margin convex, pronotum length decreases medially producing a bilobed appearance; anterolateral corners nearly right-angled, posterolateral corners broadly rounded. Fragments of four legs preserved, segment determination difficult. Elytra smooth, elongate, length 3.5× width; sutural margins straight, thin lateral rim visible on left elytron. Abdomen not preserved.

Material: Single specimen, VMNH 51912.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 12

Figure 14A–D

Description: Medium-sized beetle (6.9 mm long, 3.1 mm wide) preserved in dorsal view; preservation fair; part and counterpart. Pronotum, elytra, abdomen, and fragments of all six legs preserved. Head not visible, likely hidden beneath pronotum; possible eyes visible beneath; basal portion of both antennae preserved, segmentation obscure. Scutellum faint, ovate. Six partial legs preserved, relatively slender, all with partial femora, five with partial tibiae; hind leg on right side with three tarsal segments visible. Elytra smooth, length 3.4× width; basal margins rounded, sutural margins straight, apices pointed; thin rim along sutural margins. Abdomen visible between elytral apices; three segments preserved.

Material: Single specimen, VMNH 51273.

Comments: Specimen not identifiable beyond order; coarse preservation makes comparison to other Solite specimens difficult.

Morphotype 13

Figure 15A–D

Description: Small beetle (4.5 mm long, 2 mm wide) preserved in ventral view (counterpart in dorsal view); preservation good. Partial head, thorax, four partial legs, elytra, and abdominal sternites preserved. Head with straight anterior margin; eyes large, closely spaced. Pronotum with convex lateral margins, length ~0.7× width. Two ventral sclerites preserved: upper one quadrate, length 0.4× width; lower one triangular, corners rounded. Four partial legs preserved: two forelegs with possible femora, one middle leg with femur and partial tibia, one hind leg with tibia and/or tarsus; hind leg with fringe of fine, very faint setae along outer margin. Elytra smooth, elongate, length ~3.5× width; basal margins convex, apices pointed. Abdomen with three full sternites visible, subequal in length; apex of abdomen not preserved.

Material: Single specimen, VMNH 51271.

Comments: Specimen possibly aquatic due to fringe of hairs on hind leg, though setae are relatively short compared to those of a typical swimming fringe. Not identifiable beyond order.

Ventral preservation (and poor preservation of dorsal counterpart) makes comparison to other Solite specimens difficult.

Morphotype 14

Figure 16A–C

Description: Small beetle (3.6 mm long, 1.7 mm wide) preserved in dorsal view; preservation excellent; no counterpart. Head, both antennae, pronotum, four partial legs, elytra, and partial abdomen preserved. Head with slightly concave anterior margin and large eyes; two small palp segments visible on right side. Antennae long, filiform, both partially preserved: left with 9 segments, right with 7 segments; segment length 1.5–3× width. Pronotum slightly wider than head, posterior margin slightly wider, overall shape roughly trapezoidal. Four partial legs visible: three on right side, one on left side. Femora elongate, tibiae slender. Elytra smooth, length ~3× width, basal margins rounded, sutural margins straight, apices coming to a rounded point. Abdomen partially preserved with five segments and lateral margins visible beneath elytra.

Material: Single specimen, VMNH 51944.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit. Specimen formerly published as VMNH 3113 (Fraser et al., 2017).

Morphotype 15

Figure 17A–D

Description: Medium-sized beetle (7.8 mm long, 3.6 mm wide) preserved in ventral view; preservation excellent; part and counterpart. Head, thorax, six partial legs, and abdominal ventrites preserved. Head somewhat triangular in shape, anterior margin only partially visible, ventral details not apparent; left antenna with single basal segment preserved, right antenna filiform, 8 subequal segments visible. Prothorax rectangular, corners rounded; anterior margin slightly concave, posterior margin straight; lateral margin roughly straight; pair of circular structures posteromedially, likely procoxae; partial forefemur and foretibia visible on left side, femur stout. Meso- and metathorax preserved, margin between segments indistinct; pair of circular mesocoxae located anteromedially; mesepimeron preserved on left side, rectangular; partial femur on left side between lateral margins of pro- and mesothorax. Metathorax with elongate, transverse metacoxal plates, width of plates 2.4× length, narrowing laterally; metepisternum preserved on left side, elongate, length >4× width; partial hind femora and tibiae present, right femur 2× as long as wide, tibiae at least 7× as long as wide. Elytra mostly obscured by ventral preservation; epipleuron wide, apices pointed. Abdomen with five ventrites preserved.

Material: Single specimen, VMNH 51991.

Comments: Specimen not identifiable beyond order, though suborder Adephaga can be excluded based on ventral morphology; ventral preservation makes comparison to other Solite specimens difficult.

Morphotype 16

Figure 18A, B

Description: Small specimen (5.5 mm long, 1.8 mm wide) preserved in ventral view; preservation excellent; no counterpart. Head with partial mouthparts and antennae, thorax, six legs, and abdomen preserved. Head ovate, length roughly equal to width; anterior margin obscured by mouthparts, likely apical palp segments; eyes large, narrowly separated. Antennae long, filiform, attach just anterior to eyes: left antenna with stout scape and three slender flagellomeres; right antenna with at least nine segments, slender, elongate. Prothorax rectangular, anterior margin strongly concave, lateral and posterior margins straight; anterolateral corners bluntly pointed. Pair of triangular sclerites posteromedially, likely procoxae; forelegs with partial femora, slender tibiae, and partial tarsi

(four tarsomeres on left leg, two partial segments on right leg). Middle legs with possible coxae, partial trochanters, femora, tibiae, and partial tarsi; coxae circular, trochanters small, asymmetrically preserved; femora stout, length 3.5× width, narrowing basally; tibiae very long, slender, length ~13× width; left middle tibia covered in minute setae; left middle leg with one tarsal segment preserved, right middle leg with three full and one partial segment preserved, basal segment elongate, length almost twice that of following segments. Margin of meso- and metathorax not preserved. Middle and hind legs widely separated. Hind legs with femora and partial tibiae, proportions similar to those of middle legs; left hind leg with one partial tarsal segment. Elytral surface obscured by ventral preservation; epipleuron wide, apices bluntly pointed. Abdomen with at least four ventrites visible; concavity of segment margins increases posteriorly.

Material: Illustration and description based on VMNH 211462. One additional specimen (VMNH 95041) possibly belonging to this morphotype.

Comments: Specimen not identifiable beyond order; ventral preservation makes comparison to other Solite specimens difficult. Very similar morphology to Walnut Cove specimen VMNH 95041 (5 mm long), though coarser preservation of that specimen prevents detailed comparison.

Leehermania prorova Chatzimanolis et al., 2012

Figure 19A–F

Description: Small beetle (2.8 mm long, 0.8 mm wide, excluding terminalia) preserved in dorsal view; preservation excellent; part and counterpart. Head with eyes, mouthparts, and one antenna, pronotum, scutellum, elytra, and abdomen with terminalia preserved. Body elongate, covered in dense microsetae. Elytra rectangular, truncated, abdomen extending well beyond elytral apices. See Chatzimanolis et al. (2012) for a full description of this species.

Material: Illustration and description based on the holotype specimen, VMNH 49570. Fifty additional specimens are known: VMNH 49628, 49629, 50055, 50064, 50099, 50109, 50129, 50174, 50251, 50277, 51436, 51670, 51899, 53953, 54172, 54211, 90263, 90351, 91722, 93581, 93648, 94304, 94434, 94435, 94705, 94871, 94943, 94997, 95052, 95632, 95936, 96371, 96417, 96550, 96857, 97672, 97930, 98140, 98699, YPM IP 001147, 003131, 003146, 034677, 034689, 036447, 388866, 388885, 388907, 388914, and 527944.

Comments: There are 51 known specimens of *Leehermania* in the Solite material, all from the Cow Branch Formation. Morphotype 17 (fig. 20) is similar to this species in its shortened elytra and ringlike abdominal segments; however, differences in antennal shape indicate separate taxa. *Leehermania* was originally described as a staphylinid, but Fikáček et al. (2020) later suggested that the species belongs to an extinct lineage similar to modern Hydroscaphidae (Myxophaga) based on a number of characters, including ringlike abdominal segments lacking paratergites and compound eyes that do not protrude. Holotype specimen formerly published as VMNH 734 (Chatzimanolis et al., 2012).

Morphotype 17

Figure 20A–D

Description: Very small specimen (2.2 mm long, excluding terminalia) preserved in lateral view; preservation excellent; part and counterpart. Head with mouthparts and antennae, pronotum, three partial legs, elytra, and abdomen with terminalia preserved. Head round, probable frontoclypeal suture and pair of palps, each with two segments visible. Eyes indistinct. Antennae very well preserved, distinctly clavate; 11 segments visible on one, 9 on other; terminal three segments ~2× wider and longer than other segments and with sparse setae. Pronotum length 1.3× length of head, margins straight to slightly curved. Three partial legs (one fore,

one middle, one hind) poorly preserved, segment determination not possible. Elytra smooth, truncate, rectangular, extending just past first abdominal segment; length roughly 2.2× width. Abdomen well preserved with 6 distinct segments, apparently ringlike; 7th visible segment with lateral tergal sclerites, possibly female genitalia (as in *Leehermania*, Fikáček et al., 2020). Sparse setae scattered on abdomen and terminalia.

Material: Single specimen, VMNH 50075.

Comments: Similar in shortened elytra and ringlike abdominal segments to *Leehermania prorova* (Chatzimanolis et al., 2012; fig. 19), also from the Cow Branch Formation; however, differences in antennal shape and lack of dense setae covering body indicate separate taxa. Specimen possibly related to *Leehermania* (Myxophaga; Fikáček et al., 2020). Formerly published as VMNH 1244 (Fraser et al., 2017).

Morphotype 18

Figure 21A, B

Description: Small beetle (2.9 mm long) preserved in lateral view, preservation fair; part and counterpart. Head with mouthparts, thorax, one elytron, abdomen, and two partial legs preserved. Head roughly quadrate, anterior and posterior margins roughly straight; mandibles preserved, large, triangular, somewhat overlapping. Eyes large. Pronotum somewhat rectangular, length equal to that of head; anterior margin slightly concave, anterolateral corner rounded. Partial thorax visible beneath pronotum and elytron, at least five sclerites visible, margins faint. Two partial legs preserved: one with expanded, ovate segments, possibly femur and tibia; second also with possible femur and tibia, segments narrower than those of other leg. Elytron smooth, basal margin straight, apex broadly rounded. Abdomen apparently squashed (best viewed in counterpart); six-segmented, segments decrease in length apically.

Material: Single specimen, VMNH 95059.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit, though lateral preservation makes comparison challenging.

Morphotype 19

Figure 22A, B

Description: Very small beetle (1.9 mm long) preserved in lateral view, preservation fair; no counterpart. Partial head, pronotum, partial legs, one elytron, and partial abdomen preserved. Head poorly preserved, details indistinct. Pronotum small, lateral margin broadly rounded. Lateral portion of thorax visible, segments indistinct; one sclerite visible medially, triangular. Six partial legs preserved: one foreleg with femur and partial tibia, two fragments of other foreleg, one middle leg with femur and tibia, other middle leg with only partial femur, both hind legs with femora and tibiae; femora stout, length ~2.8× width; tibiae slender, elongate; tarsi not preserved. Elytra appear smooth, preservation coarse; anterior margin convex, lateral margin strongly concave medially, possibly an artifact of preservation; apex not preserved. Abdomen visible beneath elytron, four subequal segments preserved, apex pointed.

Material: Single specimen, VMNH 94513.

Comments: Specimen not identifiable beyond order; one of the few very small specimens in the Solite deposit; does not resemble any other Solite beetle.

Morphotype 20

Figure 23A, B

Description: Small specimen (2.5 mm long) preserved in lateral view, preservation fair; no counterpart. Head, pronotum, elytra, and partial abdomen preserved. Head with anterior and lateral margins indistinct, posterior margin straight; eyes not preserved. Pronotum length subequal to that of head; anterior margin straight, posterior margin with a concave "notch" laterally, postero-

lateral corner somewhat pointed. Elytra smooth, no microsculpture or vestiture apparent; anterior margins convex, apices bluntly pointed. Abdomen partially visible beneath elytra with at least six ventrites, apex not preserved.

Material: Single specimen, YPM IP 036445.

Comments: Specimen not identifiable beyond order; lateral preservation makes comparison to other Solite beetles difficult.

Morphotype 21

Figure 24A, B

Description: Small specimen (4.9 mm long) preserved in lateral view, preservation fair; part and counterpart. Head, pronotum, partial legs, and elytra preserved. Head with straight anterior and posterior margins; one eye visible, laterally located. Pronotum length 1.3× that of head, longest medially; anterior margin slightly concave, anterolateral corner rounded, lateral margin straight, posterolateral corner obtuse. Three partial legs and additional leg fragments preserved, legs relatively short; two forelegs with stout femora and partial tibiae; frontmost leg with quadrate trochanter and partial tarsus; middle and hind legs too fragmentary for determination of segments. Elytra apparently smooth, preservation coarse; wide lateral rim, apex broadly rounded. Abdomen not preserved.

Material: Illustration and description based on VMNH 51491. One additional specimen possibly belonging to morphotype: VMNH 50185.

Comments: Specimen not identifiable beyond order; somewhat resembles VMNH 50185, though partial preservation of that specimen makes detailed comparison difficult.

Morphotype 22

Figure 25A–C

Description: Small beetle (5.5 mm long) preserved in lateral view; preservation good; part and counterpart. Head, pronotum, five partial legs, one elytron, and abdomen preserved. Head with possible clypeus and one mandible preserved; eyes large, laterally located. Pronotum length 1.3× that of head, anterior margin straight, lateral margin convex. Five partial legs preserved: two frontmost legs with partial trochanters; all legs with elongate, slender femora and tibiae, tibiae increase slightly in width apically; hind tibia length ~9× width; hind leg also with partial tarsus, segmentation obscure. Elytron smooth, lacking microsculpture; basal margin straight, apex bluntly pointed. Abdomen with five segments visible, subequal in length; apex pointed.

Material: Single specimen, VMNH 51822.

Comments: Specimen not identifiable beyond order. Lateral preservation makes comparison difficult, but specimen does not resemble any other beetle from the Solite deposit.

Morphotype 23

Figure 26A–D

Description: Small beetle (4.8 mm long) preserved in lateral view; preservation excellent; part and counterpart. Head with mouthparts and single antenna, pronotum, partial legs, elytra, and abdomen preserved. Head large, hypognathous; single eye visible. One antenna with four segments preserved, basal two segments short, rectangular; apical two elongate. Mouthparts preserved: possible palp with at least three segments, last segment increasing in width apically; probable labium, segments indistinguishable. Pronotum subequal in length to head, margins straight to slightly curved, anterolateral corner near right-angled. Thorax visible beneath pronotum, segmentation obscure. Four partial legs preserved. One foreleg with partial femur, tibia, and tarsus; femur poorly preserved; tibia elongate, covered in very fine setae; tarsus five-segmented: first three segments short, rectangular; fourth segment elongate, with pointed lobe apically; fifth segment elongate, slender. Middle leg with trochanter, femur, and partial tibia;

trochanter circular; femur narrow basally, swollen distally; tibia elongate, with few short setae along lateral margin. Hind leg with possible trochanter, femur, tibia, and partial tarsus; trochanter faint, rounded; femur thick, not preserved basally; tibia elongate, slender; tarsus with five segments visible: first segment elongate, length at least 4× width; other segments decreasing in length apically. Three additional isolated tarsal segments visible along ventral margin of abdomen, likely from other hind leg. Elytra smooth, margins indistinct. Abdomen with six partial segments preserved.

Material: Single specimen, VMNH 97984.

Comments: Specimen not identifiable beyond order; lateral preservation makes comparison to other Solite specimens difficult.

Morphotype 24

Figure 27A–D

Description: Medium-sized beetle (12 mm long) preserved in a lateral, slightly oblique view; preservation good; part and counterpart. Head, pronotum, three partial legs, elytra, and abdomen preserved. Head with convex anterior margin; poorly preserved mouthparts (possibly mandibles) visible; eyes large, closely spaced, dorsal. Pronotum short, lateral margins not well preserved. Three partial legs visible; legs apparently short with short femora and tibiae. Fore- and middle legs with partial femora and tibiae. Hind leg with partial femur, tibia, five tarsal segments, and tarsal claw; tarsal segments subequal in length; tarsal claw about as long as tarsomeres. Elytra smooth, lacking microsculpture and vestiture; lateral rim distinct, wide; anterior margin convex, wide lateral band of sclerotization present, apex gently pointed. Abdomen fragmentary, at least three segments visible; apex indistinct.

Material: Single specimen, VMNH 49593.

Comments: Specimen probably belonging to Phoroschizidae (= Schizophoridae; Bouchard and Bousquet, 2020). Though somewhat larger in overall length, resembles Solite morphotype 25 (fig. 28). Specimen formerly published as VMNH 758 (Fraser et al., 2017).

Morphotype 25

Figure 28A, B

Description: Medium-sized beetle (>7.4 mm in length) preserved in lateral view; preservation fair; no counterpart. Head, pronotum, two partial legs, one partial elytron, and partial abdomen visible; posterior end of specimen not preserved. Head with broad anterior margin; one eye preserved, laterally located; terminal 2.5 antennal segments visible near posterolateral corner of head; terminal segment slightly conical, penultimate segment shorter. Pronotum short, broad, rectangular, margins roughly straight and wrapping laterally. Part of thorax visible below elytron. Two partial legs preserved: foreleg with femur and partial tibia; middle leg with femur, partial tibia, tarsus, and two tarsal claws; femora short, stout; middle femur subequal to length of tibia; tarsal segments indistinct. Elytron apparently smooth, lacking microsculpture and vestiture, basal margin slightly convex; thin lateral rim visible posteriorly; apex not preserved. Abdomen showing four complete segments, abdominal apex not preserved.

Material: Single specimen, AMNH 04-81.

Comments: Specimen possibly belonging to Phoroschizidae (= Schizophoridae; Bouchard and Bousquet, 2020); somewhat similar to Solite morphotype 24 (fig. 27).

Morphotype 26

Figure 29A–E

Description: Medium-sized beetle (11.4 mm long, 5.6 mm wide) preserved in dorsal view; preservation excellent; part and counterpart. Head, pronotum, scutellum, elytra, and abdomen tip preserved. Much of body covered in dense, minute, very fine microtrichia. Head trapezoidal,

roughly half the width of pronotum, medial portion raised and covered in microtrichia; anterior and lateral margins straight; eyes small, located laterally. Pronotum with slightly concave anterior margin, posterior margin convex, forming obtuse angle medially; anterolateral and posterolateral corners somewhat rounded; disc raised medially; microtrichia dense medially and thinning laterally; pronotum 0.7× width of elytra. Scutellum large, triangular; lateral margins curved; anterior margin not preserved. Elytra with dense microtrichia covering entire surface; length 2.9× width; anterior and sutural margins straight, anterolateral corners somewhat squared, apices pointed; epipleural rim very wide. Abdomen tip visible between elytral apices; at least four abdominal segments visible beneath elytra.

Material: Single specimen, VMNH 49650.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 27

Figure 30A–D

Description: Small specimen (4.3 mm long, 3.3 mm wide) preserved in dorsal and some ventral views; preservation good; no counterpart. Partial head and thorax, two leg fragments, elytra, and abdomen preserved. Head ovate, recessed beneath pronotum; eyes located laterally. Two partial leg fragments visible, elongate, possibly tibiae. Elytra covered in dense, fine, short setae; basal and sutural margins slightly convex, apices pointed, length ~2.5× width. Abdomen with five short tergites visible between elytral apices.

Material: Illustration and description based on VMNH 98157. One additional specimen possibly included in morphotype: VMNH 94100.

Comments: Specimen not identifiable beyond order; preserved in an orientation similar to that of VMNH 94100, though that specimen is slightly smaller (2.8 mm long), and setae are not clearly visible on the elytra.

Morphotype 28

Figure 31A–E

Description: Small specimen (3.9 mm long, 1.4 mm wide) preserved in an oblique, dorsal view; preservation excellent; part and counterpart. Head, two possible antennal fragments, pronotum, and elytra preserved. Head roughly oval in shape with two short, faint sutures or sulci along anterior margin; eyes large, located dorsally, very narrowly separated. Faint trace of two possible antennal segments visible above head. Pronotum roughly trapezoidal in shape, preserved asymmetrically; anterior margin straight, width increasing posteriorly, posterolateral corners curved, forming sharp points; rectangular color markings along anterior and posterior margins. Scutellum small, triangular, corners rounded. Elytra preserved obliquely, length ~3× width; anterior margins convex, lateral and sutural margins roughly straight, parallel, reaching dull point at apex. Distinct color pattern preserved; 8 melanized markings of irregular shape arranged along entire elytral surface (best seen in right elytron). Setae long, dense on markings, less dense between markings. Abdomen not visible.

Material: Single specimen, AMNH 04-57.

Comments: Specimen not identifiable beyond order. Color pattern reminiscent of some archostematans (e.g., Jarzembowski et al., 2015) and similar to that of Solite morphotypes 29 and 30 (figs. 32, 33), though pronotum differs significantly from that of morphotype 30; specimens perhaps belonging to the same or similar genera.

Morphotype 29

Figure 32A–D

Description: Small beetle (3.6 mm long, 1.4 mm wide) preserved in a dorsal, slightly oblique view; preservation excellent; part and counterpart. Head, antennae, pronotum, and elytra with color pattern and setae preserved.

Head oblong, sinuous color marking anteriorly; eyes large, located dorsally, very narrowly separated. Both antennae preserved; left antenna complete with 11 short segments, filiform; right antenna partial, six segments visible. Pronotum semicircular, width decreasing posteriorly; length 0.5× width at widest point; anterior margin straight, anterolateral corners rounded, posterior margin strongly convex. Sinuous color marking along posterior margin; color marking covered in dense setae. No scutellum visible. Elytra preserved somewhat obliquely, length ~3.2× width; anterior margins convex, lateral and sutural margins roughly straight, parallel; apex pointed. Distinct color pattern preserved; pigmented areas irregular in shape, 10 on left elytron, eight on right; covered in long, dense setae; few sparse setulae visible between pigmented areas.

Material: Single specimen, VMNH 94607.

Comments: Specimen not identifiable beyond order. Resembles Solite morphotypes 28 and 30 (figs. 31, 33) though pronotum shape differs in all three. Pattern of color markings reminiscent of some archostematans (e.g., Jarzembowski et al., 2015) and very similar to that of morphotype 30, possibly same species with proportions distorted during preservation. Specimens likely belong to the same or similar genera.

Morphotype 30

Figure 33A–D

Description: Small specimen (2.9 mm long, 1.6 mm wide) preserved in dorsal view; preservation excellent; part and counterpart. Head, pronotum, and elytra with color pattern and setae preserved. Head large, almost as wide as pronotum, anterior margin slightly concave medially; eyes large, widely separated. Pronotum short, narrow, length approximately 0.2× width; anterior margin concave, posterolateral corners not pointed; melanized marking with dense setae located centrally. Elytra ~1.7× width of pronotum, anterior margins somewhat flat, anterolateral corners broadly rounded, sutural margins straight, distal third tapering to a point at apex. Distinct, maculated color pattern preserved; ~12 melanized markings of irregular shape arranged over entire elytral surface. Setae dense on markings, very sparse between markings. Abdomen tip visible between elytral apices; broadly rounded, preservation poor.

Material: Single specimen, AMNH 04-70.

Comments: Specimen not identifiable beyond order. Elytral markings reminiscent of some archostematans (e.g., Jarzembowski et al., 2015) and similar to those of Solite morphotypes 28 and 29 (figs. 31, 32), possibly belonging to the same or similar genera, but body proportions, marking arrangement, and elytral proportions indicate separate species. Elytral markings also similar to those of one isolated elytron, Solite specimen VMNH 94027.

Morphotype 31

Figure 34A–D

Description: Small beetle (2.3 mm long, 1.2 mm wide) preserved in dorsal view; preservation excellent; no counterpart. Head with mouthparts and both antennae, pronotum, and elytra preserved. Pronotum and elytra covered in long, dense setae. Head preserved asymmetrically, anterior margin concave; eyes small, laterally located; one mandible preserved, appears bidentate. Antennae clavate, apical club three-segmented; both antennae partially preserved: left with 9 segments visible, few short setae on apical five flagellomeres; right with 5 segments preserved. Pronotum quadrate, length ~0.5× width, anterior margin straight, posterior margin obscured medially, anterolateral corners obtuse, posterolateral corners rounded; three lightly melanized areas: one circular area medially and two oblong areas laterally; pronotum covered in long, dense setae between melanized areas. Elytra smooth, lacking microsculpture; length 3× width, basal margins convex, apices obscured by dense setae arranged in rough rows; two lightly

melanized patches on each elytron: one quadrate patch anterolaterally and one ovate patch mediolaterally; melanized areas mostly lacking setae. Abdomen not visible.

Material: Single specimen, VMNH 49764.

Comments: Specimen is unique in the Solite deposit; not identifiable beyond order.

Morphotype 32

Figure 35A, B

Description: Very small specimen (1.5 mm long, 0.8 mm wide, as preserved) in dorsal view; preservation poor; no counterpart. Partial head, possible partial pronotum, and both elytra preserved. Head ovate; no eyes, antennae, or mouthparts visible. Pronotum fragmentary, poorly preserved, no details discernable. Elytra smooth, narrow, length ~2.5× width; basal and sutural margins roughly straight, apices bluntly pointed; distinct color pattern covering majority of elytral surface except at apex and in an ovate patch medially. Small portion of abdomen visible past elytral apices.

Material: Single specimen, VMNH 94723.

Comments: Specimen is unique in the Solite deposit but is poorly preserved; not identifiable beyond order.

Morphotype 33

Figure 36A–E

Description: Small beetle (3.6 mm long, 2 mm wide) preserved in dorsal view; preservation excellent, no counterpart. Head, pronotum, two partial legs, and elytra with color pattern preserved. Body generally streamlined, possibly aquatic. Head extending anteriorly, not recessed beneath pronotum; anterior margin roughly straight, lateral corners rounded; eyes large. Three complete and one partial terminal flagellomeres visible near right side of head, large. Pronotum narrow, width ~4.2× length; anterior margin concave, width ~0.6× that of posterior margin; posterior margin slightly convex; anterolateral corners pointed, posterolateral corners rounded; greatest width 0.8× elytra width. Scutellum apparently small, faint. Two partial hind legs preserved posteriorly, likely tibiae and tarsi; rightmost tibia with two distinct tibial spurs, four narrow tarsal segments, apical segment very slender; few long, fine setae closely adpressed to tarsus. Elytra smooth, no microsculpture or vestiture present; widest anteriorly with straight basal and sutural margins, apices gently pointed; length ~2.3× width; unique color pattern covering majority of elytral surface, two lighter, circular patches anteromedially; two "forks" mediolaterally, possibly veins. Abdomen tip visible between elytral apices.

Material: Single specimen, YPM IP 035981.

Comments: Specimen resembling Eucinetidae (Polyphaga), especially the genus *Noteucinetus* from New Zealand and Chile due to body shape, elytral color patterning, and the long, five-segmented hind tarsi (Bullians and Leschen, 2004); does not resemble any other beetle from the Solite deposit.

Holcoptera solitensis Thomson et al., 2017

Figures 37A–C, 38

Description: Small beetle (4.7 mm long as preserved, 2.8 mm wide) preserved in dorsal view; preservation fair; no counterpart. Peculiar specimen with body margins poorly defined, head missing. Elytra and some underlying structures preserved. Anterior portion of specimen with two symmetrical, raised circular structures laterally. Elytra with distinctive color pattern consisting of four longitudinal bands: two outer bands connecting posteriorly to form U-shape, innermost band thinner than others and extending to a color patch along the anterior margin where the orientation becomes perpendicular to the other bands. Outer elytral margins not preserved. Abdominal segments visible beneath elytra, four subequal tergites discernible; additional faint bands laterally, possibly outer margins of abdomen.

Material: Illustration and description based on VMNH 97986. Twenty-five additional specimens are known: AMNH 04-96, VMNH 49735/49736, 51498, 51511, 51839, 54135, 54136, 96728, 96729, 96731, 96736, 96762, 96765, 96766, 96768, 96769, 96782, 96784, 96787, 96789, 96791, 97234, 97243, 97247, and 97251.

Comments: There are 26 known specimens in the Solite material sharing this distinctive elytral pattern. Seven of these consist of more than a single elytron, and one specimen (VMNH 96762, fig. 37C) includes the head, though it is not attached to the body. The illustrated specimen (VMNH 97986) appears shorter than the others and is possibly longitudinally distorted. Additionally, one specimen (AMNH 04-96, fig. 38) differs in the thickness of the second innermost longitudinal band and might represent a separate species.

This morphotype was previously described as *Holcoptera solitensis* by Thomson et al. (2017) based on two isolated elytra. It should be noted that the original description states that *H. solitensis* specimens "are the only ones seen where none of the [elytral color] bands connect, either to a color patch at the base or distally" (Thomson et al., 2017: 671). The two outer bands of the Solite specimens do, in fact, connect distally, contradicting the species' original description.

Morphotype 34

Figure 39A–C

Description: Small specimen (3.9 mm long, 2.2 mm wide) preserved in dorsal view; preservation fair; no counterpart. Body generally streamlined, possibly aquatic. Pronotum and elytra visible. Head probably preserved beneath pronotum; eyes large; no other head structures apparent. Pronotum triangular, anterior margin strongly convex, posterolateral corners preserved asymmetrically, rounded; width of posterior portion subequal to width of elytra; with triangular patch of small, dense nodules posteromedially. Elytra with similar dense nodules in thin strip anteromedially; basal margins very straight, wide rim along outer elytral margins, no gap between elytral apices; two triangular areas of light sclerotization anteriorly, posterior third of elytra more heavily sclerotized; no striae or microtrichia present. Abdomen not visible.

Material: Single specimen, AMNH 04-50.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 35

Figure 40A–D

Description: Small beetle (5.2 mm long, 2.3 mm wide) preserved in dorsal view; preservation good; part and counterpart. Head, pronotum, and elytra preserved. Body ovate, streamlined, fusiform, possibly aquatic. Head somewhat triangular, anterior margin bluntly pointed, posterior margin convex; eyes large, widely separated. Pronotum semicircular in shape, anterior margin obscured by head; smooth, few very fine setae visible posteriorly and along lateral margin. Possible scutellum. Elytra elongate, length 3.3× width; basal and sutural margins straight, apices pointed; covered in dense, tiny, randomly arranged nodules; sparse, very fine setae on some areas of elytra (not figured). Partial abdomen preserved beneath elytra, four segments visible.

Material: Single specimen, VMNH 49742.

Comments: The fusiform, streamlined body shape suggests a possible aquatic lifestyle, though this is contradicted by the abundance of dense nodules covering the elytral surfaces. Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 36

Figure 41A–C

Description: Small specimen (3.9 mm long, 2.5 mm wide) preserved in dorsal view; preservation fair; no counterpart. Head, pronotum, elytra, one partial leg, and faint portion of abdo-

men preserved. Head short, broadly rounded anteriorly, posterior margin concave, right lateral margin indistinct; width roughly equal to pronotum width. Eyes widely separated, laterally situated; left eye visible, right eye not preserved. Pronotum rectangular, narrow; width 3.9× length, antero- and posterolateral corners rounded. Partial scutellum visible, small, triangular, corners pointed. Single leg fragment present between pronotum and right elytron; preservation poor. Elytra striate, six poorly preserved partial striae visible on posterolateral portion of right elytron; length roughly 2.1× width, widest medially; basal and sutural margins convex, apices bluntly pointed; thin lateral rim present along lateral margins. Abdomen faint, partially visible between elytral apices.

Material: Single specimen, AMNH 04-92.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 37

Figure 42A, B

Description: Small specimen (2.6 mm long) preserved in lateral view, preservation fair; no counterpart. Head, pronotum, two partial legs, elytra, and abdomen preserved. Head with anterior margin interrupted by simple, pointed mandibles and possible basal antennal segment; posterior margin slightly convex; eyes apparently located laterally. Pronotum length subequal to that of head; anterior margin slightly concave, lateral margin straight anteriorly but bending medially in its posterior quarter. Two partial legs preserved, both likely hind legs; one too fragmentary for determination of segments; other with partial tibia and tarsus, tarsal segmentation obscure. Elytron striate, lateral rim wide, apex broadly pointed; striae short, six visible anteriorly when specimen tilted. Abdomen visible beneath elytron, preservation poor with no segments discernable; apex apparently blunt.

Material: Single specimen, VMNH 129484.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 38

Figure 43A, B

Description: Small beetle (~2.2 mm long) preserved in lateral view, preservation good; no counterpart. Head, thorax, elytra, and abdomen preserved. Head large, poorly preserved; anterior margin with possible mandibles, frontoclypeal suture visible. Pronotum small, somewhat triangular in lateral view; anterior margin indistinct. Elytra lifted showing partial meso- and metathorax beneath. Legs not preserved. Elytra striate, length ~2.1× width; anterior margin convex, apices somewhat pointed; lateral margin of right elytron bulging in anterior third, broken in posterior third; right elytron with eight striae, left with only five visible. Abdomen extending past elytral apices, six segments preserved; segment margins indistinct medially, possibly due to membranous pleura between tergites and sternites; apex poorly preserved.

Material: Single specimen, VMNH 49659.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 39

Figure 44A, B

Description: Small specimen (3.4 mm long, 1.4 mm wide) preserved in dorsal view; preservation good, specimen symmetrical with apparently little distortion; no counterpart. Head with mouthparts, pronotum, and elytra preserved. Head with convex anterior margin; prognathous mandibles preserved; eyes large, widely separated. Pronotum roughly rectangular, length 0.7× width, without microsculpture or microtrichia; anterior margin slightly sinuous, posterior margin slightly convex; anterolateral corners pointed; incomplete median furrow distinct. Elytra stri-

ate, length 3.2× width; anterior margins convex, sutural margins straight, apices pointed; thin lateral rim visible; two partial striae preserved on right elytron, six on left elytron. Abdomen tip faintly preserved between elytral apices.

MATERIAL: Single specimen, VMNH 94814.

COMMENTS: Specimen likely belonging to Adephaga based on median longitudinal line of pronotum, striate elytra, and prognathous head. Does not resemble any other beetle from the Solite deposit.

Morphotype 40

Figure 45A–C

DESCRIPTION: Small beetle (3 mm long, 1.2 mm wide) preserved in dorsal view; preservation good; no counterpart. Head, pronotum, and elytra preserved. Head with broadly rounded anterior margin, posterior margin roughly straight; eyes, mouthparts, and antennae not preserved. Pronotum quadrate, subequal to head in width; anterior margin straight, posterior margin convex, anterolateral corners rounded, posterolateral corners slightly pointed, disc raised medially. Scutellum faint, triangular. Elytra elongate, length 3.6× width; anterior margins rounded, sutural margins straight, apices bluntly pointed; eight distinct striae visible, roughly parallel, apparently converging at anterior and posterior ends. Abdomen not visible.

MATERIAL: Single specimen, AMNH 04-89.

COMMENTS: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 41

Figure 46A–D

DESCRIPTION: Small beetle (~5.6 mm long) preserved in lateral view; preservation excellent; part and counterpart. Head, one antenna, complete thorax, elytra, abdomen, and two partial legs preserved. Head of roughly equal length to pronotum; eyes indistinct; possible mouthpart extending anteriorly. Antenna with 8 segments visible, segments 5–7 (as preserved) distinctly cordate, gradually increasing in width distally. Pronotum with lateral area raised or swollen. Two partial legs preserved: one with small triangular trochanter, femur, and partial tibia; other with only partial femur preserved. Elytra not covering entire abdomen; striate, left elytron with at least 9 partial striae; area near anterolateral corner slightly elevated; elytral apex narrowed, rounded. Elytra lifted, showing partial meso- and metathorax beneath. Abdomen with six segments exposed, lateral margins of tergites and sternites visible; abdominal tip large and pointed, possibly telescoped and distended.

MATERIAL: Single specimen, YPM IP 036434.

COMMENTS: Specimen not identifiable beyond order and does not resemble any other beetle from the Solite deposit.

Morphotype 42

Figure 47A–C

DESCRIPTION: Small specimen (3.2 mm long, 1.4 mm wide) preserved in dorsal view; preservation good; no counterpart. Head, partial antenna, pronotum, two partial legs, elytra, and possible abdomen tip preserved. Head somewhat triangular in shape with irregular anterior margin and semicircular frontoclypeal suture; eyes large and closely spaced. Left antenna filiform with seven partial segments preserved, little to no variation in segment widths; right antenna fragmentary with only two flagellomeres visible. Pronotum about half as long as wide, narrower than elytra, rectangular in shape with rounded corners and raised disc; incomplete median furrow prominent. Two partial femora preserved on right side of body. Elytra elongate, length roughly 3× width; basal margins rounded, apices bluntly pointed; thin lateral rim visible on distal half of left elytron. Elytra possibly striate, three very faint striae visible on right elytron near sutural margin. Partial abdomen tip protruding beyond apex of right elytron.

Material: Single specimen, VMNH 50226.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 43

Figure 48A–D

Description: Small specimen (5.2 mm long, 2.1 mm wide) preserved in dorsal view; part and partial counterpart. Head, pronotum, four partial legs, and elytra preserved. Head large, anterior margin poorly preserved; eyes small, widely separated, shape somewhat distorted. Pronotum generally rounded, approximately 0.6× width of elytra, with distinct posterolateral projections as in Elateridae; anterior margin poorly preserved but probably overlapping posterior portion of head; incomplete median furrow distinct. Four partial legs preserved: portions of all three legs visible on right side, only forefemur and foretibia preserved on left side. Possible tarsal claws on right foreleg. Elytra elongate, length 3.2× width, basal margins transverse, lateral margins straight and roughly parallel in basal half, tapering to a point at apices; thin lateral rim, few striae visible near sutural margin. Partial abdomen visible between elytra.

Material: Single specimen, VMNH 50190.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit. Specimen formerly published as VMNH 1359 (Fraser et al., 2017).

Morphotype 44

Figure 49A, B

Description: Small beetle (4.6 mm long, 1.8 mm wide) preserved in dorsal view; preservation poor; no counterpart. Head, pronotum, two leg fragments, elytra, and partial abdomen preserved. Body slender. Head somewhat triangular, length roughly equal to width, anterior margin tapering to a broad, rounded point; possible eye preserved on right side. Pronotum long, quadrate, length 0.7× width; anterior margin concave, anterolateral corners sharply pointed. Two leg fragments visible on left side between pronotum and elytron, possibly femora. Elytra striate, narrow, length ~3.6× width; anterior margins slightly convex, sutural margins straight, apices broadly rounded; few thin striae visible medially, faint. Abdomen partially visible beneath left elytron, three segments preserved.

Material: Single specimen, VMNH 93596.

Comments: Specimen not identifiable beyond order. Somewhat similar in proportions and pronotum shape to VMNH 53904 (~4.8 mm long, 1.9 mm wide), though poor preservation of that specimen makes detailed comparison difficult.

Morphotype 45

Figure 50A–E

Description: Small beetle (3.3 mm long, 1 mm wide) preserved in dorsal view (counterpart in ventral view); preservation good. Head with antennae, pronotum, three partial legs, elytra, and partial abdomen preserved. Body elongate. Head dome shaped, anterior margin strongly convex; eyes small, laterally located. Antennae moniliform to slightly clavate, 11-segmented, apical three flagellomeres slightly larger than others. Pronotum quadrate, length 0.8× width; anterior and posterior margins slightly convex, antero- and posterolateral corners rounded; disc raised in center. Possible scutellum preserved, faint. Three legs partially visible, largely hidden beneath body. Elytra striate; elongate, length ~4.6× width; anterior margins rounded, sutural margins straight, apices bluntly pointed; striae thin, faint, at least eight visible medially on right elytron. Abdomen protruding slightly past elytral apices; three segments visible beneath elytra.

Material: Single specimen, VMNH 91682.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 46

Figure 51A–C

DESCRIPTION: Medium-sized beetle (8 mm long, 3.5 mm wide) preserved in dorsal view, preservation good; no counterpart. Head with partial antennae, thorax, four partial legs, and elytra preserved. Body elongate. Head square, anterior margin straight, posterior margin not preserved; eyes widely separated, laterally located. Both antennae partial; left with seven segments preserved; segments somewhat moniliform, basal ones slightly longer than wide, apical ones broader; right antenna with only two partial segments visible. Pronotum roughly circular, anterior and posterior margins obscure; visible anterolateral corner broadly rounded. Four partial legs preserved, all with femora and tibiae, no tarsi; femora stout; tibiae short and stout, length 3.8× width; middle tibia with a few fine setae along margins. Elytra striate, anterior margins convex, anterolateral corners broadly rounded, sutural margins indistinct; elytral apices not preserved; epipleural rim broad, wider than distance between striae. Elytron with six distinct striae, converging toward apex, only visible when specimen viewed at an angle. Abdomen not preserved.

MATERIAL: Single specimen, YPM IP 388741.

COMMENTS: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 47

Figure 52A–D

DESCRIPTION: Small beetle (5.7 mm long) preserved in dorsal view; preservation good; no counterpart. Head, pronotum, elytra, and abdomen preserved. Head long, somewhat triangular, clypeal suture faint; mandibles preserved, triangular. Eyes large, laterally located; one possible antennal segment preserved on right side of head. Pronotum uniquely shaped, length and width increasing medially; anterior margin straight medially, anterolateral corners bluntly pointed; posterior margin very strongly convex; posterolateral corners rounded. Scutellum small, triangular, width 2× length. Elytra striate, without punctations or setulae; length ~2.3× width, anterior margins straight, sutural margins convex, apices sharply pointed; thin rim along sutural margins; striae faint, seven visible on right elytron, five on left. Abdomen poorly preserved, five segments visible.

MATERIAL: Illustration and description based on VMNH 129485. One additional specimen possibly included in morphotype: VMNH 97637 (fig. 52D).

COMMENTS: Specimen not identifiable beyond order. Resembles Cow Branch specimen VMNH 97637 in pronotum shape and overall size, though preservation of VMNH 97637 is fragmentary and striae are not evident.

Morphotype 48

Figure 53A–C

DESCRIPTION: Small beetle (5 mm long, 2.6 mm wide) preserved in dorsal view with some relief; preservation excellent; part and counterpart. Head, one partial antenna, pronotum, and elytra preserved. Head partially recessed beneath pronotum; anterior margin convex. Eyes large, laterally located and not protruding. One partial antenna with at least 4 segments visible on right side of head, possibly clavate. Pronotum with concave anterior margin and convex posterior margin, posterior margin slightly pointed medially; anterolateral corners sharply pointed, posterolateral corners rounded; disc raised medially, rim present near lateral margins; pronotum ~0.8× width of elytra. Elytra striate, length 2.75× width; anterior margins flat, anterolateral corners distinctly squared, sutural margins straight, apices bluntly pointed; raised, rounded areas present anterolaterally; epipleural rim distinct, narrowing posteriorly; thin sutural margin visible; seven distinct striae, roughly parallel, converging at anterior and posterior ends. Abdomen tip visible between elytral apices.

Material: Illustration and description based on VMNH 49781. Morphotype includes one additional specimen: VMNH 129489.

Comments: Very similar to Solite specimen VMNH 129489, except in shape of anterolateral pronotal corners, which are more rounded in VMNH 129489; possibly belonging to same species. Specimen most resembles Phoroschizidae (= Schizophoridae; Bouchard and Bousquet, 2020) in body shape and proportions; however, phoroschizids possess long filiform antennae and lack distinct elytral striae. Very similar in size, shape, and proportions to middle Permian *Archosyne permiana* of China and the Lower Liassic specimens "Carabidae (?)" (In.49572; fig. 53D) and "Dryopoidea (?)" (In.59101, In.51009; In.64024, fig. 53E) of Dorset, England (Whalley, 1985: figs. 70, 73–75).

Morphotype 49

Figure 54A–D

Description: Small specimen (4.2 mm long, 2.6 mm wide) preserved in dorsal view; preservation good; no counterpart. Head, pronotum, and elytra preserved. Head somewhat triangular, anterior margin strongly convex. Eyes apparently small, laterally located. Pronotum preserved irregularly, width 3.5× length; anterior margin concave, posterior margin slightly sinuous, convex, widest medially; anterolateral corners preserved asymmetrically, somewhat pointed forward; posterolateral corners curving anteriorly; pronotum width subequal to elytra width. Elytra striate, length roughly 2.4× width; wide epipleural rim forming distinctly squared, shoulderlike anterolateral corners, rim narrowing posteriorly; sutural margins straight, apices bluntly pointed; seven distinct, fairly deep striae, roughly parallel, converging at posterior end, lateral two on right elytron connected anteriorly. Abdomen not visible.

Material: Single specimen, VMNH 53851.

Comments: Specimen not identifiable beyond order. Generally similar in shape, proportions, and striate elytra with squared anterolateral corners to Solite morphotype 48 (fig. 53), possibly belonging to related taxa. Specimen formerly published as VMNH 129 (Fraser et al., 2017).

Morphotype 50

Figure 55A–E

Description: Small beetle (4.3 mm long, 2.3 mm wide) preserved in dorsal view; preservation excellent; part and counterpart. Head, pronotum, six legs, elytra, and partial abdomen preserved. Head oblong, anterior margin convex, eyes located laterally; possible frontoclypeal suture visible. Pronotum roughly rectangular with rounded corners, length 2.5× width, anterior margin concave. Scutellum small, triangular, corners rounded. All legs at least partially preserved. Left foreleg: partial tibia, small tibial spur, at least two short tarsal segments, and two small tarsal claws preserved; small, pointed lobe projecting from tarsal segment near base of tibia. Right foreleg: partial tibia, small tibial spur, at least two tarsal segments and two small tarsal claws visible. Left middle leg: partial tibia, fragmentary tarsus. Right middle leg: partial tibia, small, ventral tibial spur, at least two tarsal segments (basal segment ~2× length of other), and two small tarsal claws visible; tibia with few setae located medially and with distinct fringe of setae along anterior margin. Left hind leg: partial tibia only. Right hind leg: partial tibia, three tarsal segments, two small tarsal claws preserved; few isolated setae near apical margin of tibia. Elytra with 10 distinct striae (when viewed obliquely), converging toward apex; basal margins straight to slightly curved, sutural margins convex, apices tapering to a blunt point; elytra length ~2.6× width. Three abdominal segments visible between elytra.

Material: Single specimen, VMNH 49790.

Comments: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit. Specimen formerly published as VMNH 959 (Fraser et al., 2017).

Morphotype 51

Figure 56A–D

Description: Small beetle (4.3 mm long, 2.1 mm wide) preserved in dorsal view; preservation good; part and counterpart. Head, pronotum, two partial legs, elytra, and abdomen tip preserved. Head roughly rectangular; anterior margin slightly convex. Eyes poorly preserved, likely laterally located. Pronotum somewhat rectangular, width 1.9× length; anterior margin concave laterally and convex medially; posterior margin slightly convex; anterolateral corners bluntly pointed, posterolateral corners broadly rounded; pronotum ~0.8× width of elytra. Two partial leg segments preserved, slender, likely middle femora; right segment with fine setae on apical margin. Elytra striate, length ~2.9× width; anterior and sutural margins convex, apices bluntly pointed; eight distinct striae, curving outward, medial striae apparently converging; outermost stria forming a raised shelf. Few sparse setae on posterior end of elytra (not figured). Abdomen tip visible between elytral apices.

Material: Illustration and description based on VMNH 51831. Two additional specimens possibly included in morphotype: VMNH 54562 and 95080.

Comments: Generally similar in habitus to Solite morphotype 48 (fig. 53). Outward-curving striae similar to those of isolated elytral morphotypes 89, 90, and 91 (figs. 77G–L). Specimen most resembles Phoroschizidae (= Schizophoridae; Bouchard and Bousquet, 2020) in body shape and proportions; however, phoroschizids lack distinct elytral striae.

Morphotype 52

Figure 57A–D

Description: Small beetle (2.7 mm long, 1.2 mm wide) preserved in dorsal view; preservation fair; part and counterpart. Partial pronotum, three partial legs, elytra, and abdomen preserved. Head not visible. Pronotum fragmentary, somewhat hexagonal in shape as preserved; anterior and lateral margins indistinct; visible posterolateral corner right-angled, posterior margin angular, pointed medially. Three partial legs preserved: foreleg with femur and partial tibia; middle leg with femur, tibia, and one tarsal segment; hind leg with femur and partial tibia; femora stout, width 3× that of tibiae; tibiae long, slender, middle tibia length 11.3× width. Elytra striate, length ~3.5× width; anterior margins broadly rounded, apices sharply pointed; eight striae visible on left elytron, nine on right; striae roughly parallel, evanescent apically; when tilted, elytra appear reticulate with short, irregular crossveins. Abdomen visible beneath elytra, four tergites preserved, apex rounded.

Material: Single specimen, VMNH 51649.

Comments: Counterpart to VMNH 51651. Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 53

Figure 58A–C

Description: Small specimen (2.2 mm long, 1.2 mm wide) preserved in dorsal view; preservation fair; no counterpart. Pronotum and elytra preserved. Head not visible. Pronotum preserved asymmetrically, broad with strongly convex anterior and posterior margins, faint anterolateral lobes; posterolateral corners hidden beneath elytra; disc raised medially. No scutellum visible. Elytra striate, elongate, length ~3.2× width; anterior margins rounded, sutural margins straight in basal half, apices bluntly pointed; thin rim along lateral and sutural margins; eight distinct striae visible, parallel, bending posteriorly toward sutural margin; fine, faint, slightly irregular cells visible on entire elytral surface when specimen tilted, cells larger and more irregular posteriorly. Abdomen not preserved.

Material: Illustration and description based on YPM IP 016827. Morphotype includes one additional specimen: VMNH 49635.

Comments: Specimen not identifiable beyond order. Very similar in proportions to Solite specimen VMNH 49635.

Morphotype 54

Figure 59A–C

Description: Very small specimen (>1.7 mm long) preserved in a dorsal, somewhat oblique view; preservation good; no counterpart. Pronotum, elytra, and abdomen preserved. Head not visible. Pronotum approximately rectangular, length 0.5× width; anterior margin obscured medially, posterior margin slightly convex; disc somewhat raised medially. No scutellum visible. Elytra striate, reticulate; preserved asymmetrically and at an angle: left elytron with length 2× width, right elytron with length 3.1× width; anterior margins broadly rounded, sutural margins convex, apices pointed; thin, well-defined rim along lateral and sutural margins; nine distinct striae visible, absent basally, converging toward apex; reticulations formed by crossveins between striae, best viewed when specimen tilted. Abdomen visible between spread elytra, five distinct tergites present; apex broadly rounded.

Material: Single specimen, VMNH 92751.

Comments: Specimen not identifiable beyond order; similar reticulated elytral pattern also present in isolated elytron morphotype 98 (figs. 59D, 79) from the Walnut Cove Formation, though isolated elytron is slightly larger (by ~1 mm in length).

Morphotype 55

Figure 60A–E

Description: Small beetle (3 mm long excluding abdomen, 1.8 mm wide) preserved in dorsal view; preservation excellent; part and counterpart. Partial head, pronotum and elytra with color pattern, and partial abdomen preserved. Head partially obscured, roughly half the width of pronotum; eyes located laterally. Pronotum as wide as elytra; anterior margin concave; visible anterolateral corner pointed, curving slightly inward toward head; posterolateral corners rounded and bending posteriorly toward elytra; irregularly shaped melanized marking medially. Elytra with straight basal and sutural margins, apices indistinct; length ~2.3× width; unique color pattern covering posterior two-thirds and forming two branches in anterior third; five rows of punctures near lateral elytral margins; thin rim along lateral margins. Abdomen with at least five segments visible between elytra; posterior margin not preserved.

Material: Illustration and description based on YPM IP 016828. Two additional specimens included in morphotype: VMNH 49762 (fig. 60E) and 51687.

Comments: YPM IP 016828 is counterpart to specimen YPM IP 036446. Specimen not identifiable beyond order; possibly belonging to same genus or species as Cow Branch specimens VMNH 51687 and VMNH 49762 (fig. 60E); color pattern also similar to that of Cow Branch specimen VMNH 94739, though body proportions differ slightly.

Morphotype 56

Figure 61A–D

Description: Small beetle (5.9 mm long, 4.5 mm wide) preserved in dorsal and some ventral views; preservation good; no counterpart. Head and thorax partial; elytra fully preserved. Head apparently recessed beneath pronotum, only ovate eyes visible beneath. Pronotum with anterior margin strongly convex, posterior margin straight, posterolateral corners acutely pointed; no microsculpture or fine punctation. Segment posterior to pronotum poorly preserved, likely mesothorax, with pair of circular structures, probably coxae, visible posteromedially. Elytra with somewhat straight basal margins, apices pointed, narrow lateral rim present; length 2.2× width; covered in fine, dense punctures except for in small area near depressed, anterolateral ledge on each elytron. Abdomen not preserved.

MATERIAL: Single specimen, VMNH 129481.

COMMENTS: Specimen not identifiable beyond order; does not resemble any other beetle from the Solite deposit.

Morphotype 57

Figure 62A–D

DESCRIPTION: Medium-sized specimen (7.7 mm long, 2.8 mm wide); head preserved in dorsal view, thorax and abdomen preserved in ventral view; preservation good; part and counterpart. Head, antennae, pronotum, four partial legs, and partial elytra preserved. Head elongate, roughly rectangular; preocular portion short-rostrate; poorly preserved prognathous mouthparts extend anterior to antennae, three partial palp segments visible on left side; eyes distinct, laterally located. Both antennae well preserved, filiform, segment widths roughly equal; 9 segments visible on left antenna, 11 segments on right; third visible antennomere at least 2× length of others. Pronotum roughly 0.5× width of elytra, rounded anteriorly, with two pairs of symmetrical, parallel grooves present; posterolateral corners extended into thick, blunt points. Four partial legs preserved, femora distinctly swollen, appear cursorial. Left middle leg: femur and tibia preserved. Right middle leg: partial femur and four partially disarticulated tarsal segments preserved. Left hind leg: trochanter, femur, tibia, and tarsus with five tarsomeres visible; femur swollen centrally; tibia slender, simple; basotarsomere length ~2× that of second tarsomere. Right hind leg: trochanter, femur, and partial tibia preserved. Three additional leg fragments (possibly tarsi) overlying left side of abdomen. Elytra obscured by ventral preservation; epipleuron wide. Abdomen poorly preserved, segments indistinct.

MATERIAL: Single specimen, VMNH 97968.

COMMENTS: Specimen reminiscent of Obrieniidae Zherikhin and Gratshev, 1993 (Archostemata; Gratshev and Zherikhin, 2003) in body proportions and elongate head; most resembles Jurassic species *Kararhynchus occiduus* Zherikhin and Gratshev, 1993 in habitus (see also Legalov, 2012). However, the Solite specimen's larger size, shorter rostrum, and filiform antennae differ from Obrieniidae. Specimen does not resemble any other beetle from the Solite deposit. Formerly published as VMNH 838 (Fraser and Grimaldi, 2003; Fraser et al., 2017).

Morphotype 58

Figure 63A, B

DESCRIPTION: Medium-sized beetle (8.9 mm in length) preserved in lateral view; preservation good; no counterpart. Head, pronotum, five partial legs, elytra, and partial abdomen preserved. Head with blunt anterior margin; preocular area expanded, length equal to eye diameter; both eyes preserved, located laterally; antennae fragmentary: two segments of right antenna preserved, segment two 0.4× width of basal segment, basal segment short indicating antennae not geniculate; six segments of left antenna preserved, subequal in length and width. Pronotum small, roughly trapezoidal, length 1.2× that of head; anterior margin straight, posterior margin irregular. Five partial legs preserved: one too fragmentary for segment determination; two forelegs, one with small, quadrate trochanter, femur, and two tarsal segments, other with femur and tibia; one middle leg with femur, tibia, two partial tarsal segments, and two tarsal claws; one hind leg with femur, tibia, and two fragmentary tarsi. Femora elongate, length ~7× width, swollen medially; tibiae also elongate, length ~12× width. Elytra punctate, convex with six rows of deep, circular punctures, distance between punctures greater than puncture diameter; basal margins obscured by pronotum, apices pointed; two rectangular, melanized bands medially. Possible abdomen visible beneath elytra, preservation poor, segmentation indistinct.

MATERIAL: Single specimen, VMNH 92743.

Comments: Specimen is very weevillike: it has an expanded preocular area, convex elytra with rows of punctures, and swollen femora. However, diagnostic features of the group are not preserved (e.g., pseudotetramerous tarsal structure of Phytophaga [Svacha and Lawrence, 2014]; geniculate antennae with compact antennal clubs as in most Curculionoidea, and radial sclerites on hind wings [Oberprieler, 2014]). Specimen is unique in the Solite deposit.

Morphotype 59

Figure 64A–E

Description: Medium-sized beetle (7.2 mm long) preserved in dorsal view, preservation excellent; part and partial counterpart. Head, thorax, four partial legs, elytra, and abdomen preserved. Body elongate. Head rectangular, length 1.1× width, anterior and posterior margins roughly straight; prognathous, mandibles slightly projecting, visible at anterior margin of head; eyes preserved; one partial antenna with four basal segments visible, segments short, compact, first segment roughly twice the width of others. Pronotum roughly square, width 1.3× length, antero- and posterolateral corners convex; lateral rim present; pronotum covered in faint microsculpture. Four partial legs preserved: one fragmentary foreleg with femur and tibia; one small fragment of middle leg; two partial hind legs, each with short trochanters and partial femora. Elytra with fine punctures arranged in narrow columns, no scales or microsetae; basal and sutural margins convex, apices rounded; epipleuron thick, with faint microstructure. Abdomen with five segments visible between spread elytra, apex rounded.

Material: Single specimen, YPM IP 016838.

Comments: Specimen generally similar in habitus to Ommatidae (Archostemata) but lacks scalelike setae on elytra. Does not resemble any other beetle from the Solite deposit. Specimen formerly misidentified as Adephaga in Grimaldi and Engel (2005).

Morphotype 60

Figure 65A–F

Description: Medium-sized beetle (12.7 mm long, 3.8 mm wide) preserved in possible ventral view, preservation excellent; part and partial counterpart. Head, thorax, fragmentary legs, elytra, and abdomen preserved. Body elongate, much of surface covered in small nodules. Head narrow, length roughly 1.6× width, preocular area extended with distinct median furrow and two large paramedian swellings ventrally; one eye preserved, small, located laterally; one partial antenna near anterior margin of head, four small segments visible. Pronotum asymmetrically preserved, corners rounded, width 1.8× that of head; covered in small nodules. Four partial legs: one fragmentary foreleg; one middle leg with tibia and partial tarsus, one tibial spur visible, tarsal segments obscure; two partial hind legs, each with short, rounded coxa, and one with partial femur. Elytra partially preserved, left elytron revealing straight sutural margin and coarse punctures or small cells arranged in five partial rows (between veins), small nodules in narrow rows apically; lateral rim thick, small nodules throughout; elytral apices rounded. Abdomen with five segments visible, apex gently pointed.

Material: Single specimen, AMNH 04-59.

Comments: Specimen belonging to suborder Archostemata, possibly to family Cupedidae. Head structure similar to *Notocupes rostratus* (Ponomarenko, 1969). Does not resemble any other beetle from the Solite deposit.

Morphotype 61

Figures 66A, B, 67A–E

Description: Very large specimen (>33 mm long, 9.3 mm wide) preserved in a dorsal, somewhat oblique view; preservation good; part and counterpart. Body elongate, covered in dense, fine nodules. Head with mouthparts, pronotum, scutellum, three partial legs, and

elytra preserved. Head prognathous; mandibles large, elongate, cone-shaped, length 1.7× that of head; clypeus and/or labrum filling space between mandibles. Eyes small, widely separated. Pronotum roughly rectangular, length 0.6× width; anterior margin straight, lateral margins irregular, posterior margin straight medially and concave laterally; anterolateral corners pointed. Scutellum heart shaped. Three partial legs preserved: one disarticulated leg anterior to head, possible femur and tibia; one foreleg with partial femur, tibia, and tarsus; tarsus with five segments of differing lengths, apical segment the longest, bilobed; one fragment of middle or hind leg overlapping elytron, possibly femur. Elytra elongate, covered in dense, fine nodules; anterior margins strongly convex, sutural margins straight, apices not preserved. Abdomen faint, two segments visible beneath elytra.

Material: Single specimen, VMNH 49597.

Comments: Not identifiable beyond order. Specimen is unique; does not resemble any other beetle from the Solite deposit. Specimen is among the largest articulated insects known from the Solite deposit; only one other specimen reaches ~30 mm in length: VMNH 97999, a possible neuropteran.

Elytral Morphotype Accounts

Morphotype 62

Figure 68A, B

Description: Complete elytron (no counterpart) from the Walnut Cove Formation. Small (2.1 mm long, 1 mm wide), unornamented; preservation good, preserved without relief. Asymmetrical, length 2.1× width, basal half subequal in width. Basal margin nearly straight, corners rounded, apex broadly rounded. Sutural margin straight, lateral margin strongly curved. Thin lateral rim. No striae, punctation, ornamentation, or microstructure apparent.

Material: Single specimen, VMNH 97505.

Morphotype 63

Figure 68C, D

Description: Complete elytron (part and counterpart) from the Cow Branch Formation. Small (1.8 mm long, 0.8 mm wide), unornamented; preservation good, preserved without relief. Asymmetrical, length roughly 2.3× width, widest medially. Basal margin straight, baso-lateral corner rounded and obtuse, baso-sutural corner right-angled, sutural margin convex, apex pointed. Thin lateral rim. No striae, ornamentation, or microstructure.

Material: Illustration and description based on VMNH 99030. Two additional specimens possibly belonging to this morphotype: VMNH 50114 and VMNH 99031.

Comments: Very similar in size and shape to VMNH 99031 (1.7 mm long, 0.8 mm wide), which is about 6 mm away on the same slab; likely from same species or individual.

Morphotype 64

Figure 68E, F

Description: Elytron (no counterpart) from the Walnut Cove Formation. Small (2.3 mm long, 1.2 mm wide), unornamented; concave in relief with inner surface visible, preservation fair. Symmetrical, almond shaped, widest medially, length roughly 1.9× width. Basal margin gently curved, lateral and sutural margins strongly convex, corners poorly preserved, apex bluntly pointed. No lateral rim. No striae or ornamentation apparent.

Material: Single specimen, VMNH 95504.

Comments: Shape and proportions similar to elytra of articulated Solite morphotype 6 (1.2 mm long, 0.6 mm wide; fig. 8), though slightly larger in size and lacking the fine setae found in morphotype 6.

Morphotype 65

Figure 68G, H

Description: Complete elytron (no counterpart) from the Walnut Cove Formation. Small

(4.1 mm long, 1.7 mm wide), unornamented; preservation good, preserved without relief. Roughly symmetrical, widest medially; length 2.4× width. Basal margin rounded, corners obtuse, lateral and sutural margins convex, apex rounded. No lateral rim. Possible tubular vein basally. No striae or ornamentation apparent.

Material: Single specimen, VMNH 97607.

Morphotype 66

Figure 68I, J

Description: Complete elytron (part and counterpart) from the Walnut Cove Formation. Small (2.9 mm long, 1.2 mm wide), unornamented; preservation good, preserved without relief. Elongate, symmetrical, length 2.4× width, basal half subequal in width, narrowing significantly toward apex. Basal margin nearly straight, corners rounded, lateral margins slightly convex, apex sharply pointed. Slight lobe along mediolateral margin; thin lateral rim along opposite side. No striae or ornamentation apparent.

Material: Single specimen, VMNH 97319.

Morphotype 67

Figure 68K, L

Description: Elytron (no counterpart) from the Walnut Cove Formation. Small (1.6 mm long, 0.5 mm wide), unornamented; preservation good, strongly concave in relief. Elongate, asymmetrical, length roughly 3.2× width, narrowing significantly toward apex. Basal margin partially obscured by matrix, appears rounded; lateral margins slightly convex, apex pointed; distinct lobe present along upper margin. Thin lateral rim along basal margin; possible vein along posterior two-thirds of margin, slender, tubular. Large depression anteriorly. No striae or ornamentation apparent.

Material: Illustration and description based on VMNH 97104. One additional specimen possibly belonging to this morphotype: VMNH 94895.

Comments: Similar to VMNH 94895 (1.6 mm long, 0.5 mm wide) in size, shape, and presence of lobe along lateral margin. Two articulated morphotypes also share a similar elytral lobe: morphotypes 38 and 54 (figs. 43, 59). Their elytra are of similar size (1.5–1.6 mm in length); however, they are striate and reticulated, respectively.

Morphotype 68

Figure 69A, B

Description: Complete elytron (part and counterpart) from the Cow Branch Formation. Small (2 mm long, 0.7 mm wide), with color pattern; preservation good, preserved without relief. Asymmetrical, length 2.9× width, widest medially. Basal margin nearly straight, visible basolateral corner rounded, lateral margins convex, apex bluntly pointed. No lateral rim. Color pattern distinct.

Material: Single specimen, VMNH 54567.

Comments: A few other Solite specimens have color patterns on their elytra, but the pattern of this specimen is unlike that of any other in the deposit.

Morphotype 69

Figure 69C, D

Description: Fragmentary elytron (no counterpart) from the Walnut Cove Formation. Small (3.6 mm long, 1.1 mm wide, as preserved), covered in large nodules; preservation fair, preserved without relief. Elongate, parallel sided; narrow, width subequal throughout. Basal margin not preserved, one lateral margin irregular, apex obscured by matrix. Small section of lateral rim visible anteriorly. Covered in nodules, nodules large (~0.07 mm diameter) relative to size of elytron, distinct, circular or ovate; arranged in 8 rows, decreasing in size apically; space between nodules roughly equal to nodule diameter.

Material: Single specimen, VMNH 95448.

COMMENTS: Nodular elytra are uncommon; specimen is unlike any other in the Solite deposit.

Morphotype 70

Figure 69E–G

DESCRIPTION: Complete elytron (no counterpart) from the Walnut Cove Formation. Small (3.3 mm long, 1.3 mm wide), covered in prominent nodules; preservation good, preserved without relief. Ovate, nearly symmetrical, length 2.5× width; widest medially, tapering basally and apically. Basal margin straight; corners asymmetrical, one right-angled, other obtuse; lateral margins convex, apex broadly rounded. Fragmentary lateral rim visible along one margin, thin. Loss of carbon film producing faux color pattern. Nodules prominent, circular, raised like small pedestals; arranged in 10 rows, distance between nodules slightly greater than nodule diameter.

MATERIAL: Illustration and description based on VMNH 95487. Three additional specimens possibly belonging to this morphotype: VMNH 95602, 97427, and 98236.

COMMENTS: The nodules of this specimen are very unique. A few other specimens from the Walnut Cove Formation have a similar arrangement of potential nodules (VMNH 95602, 97427, and 98236). Four slightly smaller specimens (VMNH 96875, 97151, 98311, and 98312) also have a similar appearance.

Morphotype 71

Figure 70A, B

DESCRIPTION: Fragmentary elytron (no counterpart) from the Walnut Cove Formation. Medium sized (8.2 mm long, 2.4 mm wide, as preserved), covered in dense nodules; preservation fair, preserved without relief. Elongate; basal margin and apex not preserved. Lateral rim along one margin, thick, distinct. Entire elytral surface covered in dense nodules producing "bumpy" appearance; nodules circular, very densely packed; three distinct lines of nodules visible in basal half of elytron, probably veins.

MATERIAL: Single specimen, VMNH 97492.

COMMENTS: This specimen is unique in the Solite deposit.

Morphotype 72

Figure 71A, B

DESCRIPTION: Fragmentary elytron (part and counterpart) from the Walnut Cove Formation. Medium sized (6.4 mm long, 3.1 mm wide, as preserved), with window punctures; preservation good, preserved without relief. Somewhat symmetrical in preserved portion; basal margin not preserved, lateral margins convex, apex bluntly pointed. Wide lateral rim along one margin. Window punctures large (up to 0.25 mm in diameter), irregularly shaped, polygonal; arranged in approximately 10 rows, distance between punctures varies.

MATERIAL: Single specimen, VMNH 49731.

COMMENTS: Counterpart of specimen VMNH 95436. Similar to Early Jurassic (Sinemurian-Toarcian) *Zygadenia westraliensis* of Western Australia (Martin, 2010: fig. 2b; fig. 71C herein; >4.3 mm long, 2.5 mm wide). Also similar in size and shape to Species 20 (6 mm long) of Papier et al. (2005) from the Anisian of France; however, the punctures of the French specimen are more densely packed. Specimen is unique in the Solite deposit and likely belongs to suborder Archostemata due to the presence of window punctures.

Morphotype 73

Figure 71D, E

DESCRIPTION: Two fragmentary, partially overlapping elytra (no counterpart) from the Cow Branch Formation, seemingly poorly sclerotized. Medium sized (>7.6 mm long, as preserved), with large, latticelike cells; preservation fair. Basal margins and apices not preserved, no lateral rim visible. Cells large (~0.14 mm diameter) but decreasing in size apically, polygonal,

arranged in rows forming reticulate pattern; cell preservation differs on each elytron: cells of right elytron have a more three-dimensional appearance, cells of left elytron appear flatter.

Material: Single specimen, VMNH 94836.

Comments: This specimen is unique in the Solite deposit; no other Solite specimens share its apparently poor sclerotization or latticelike cells. These elytra appear to most resemble those of living members of the family Cupedidae (Suborder Archostemata). Original specimen could not be located; specimen was examined from a photo.

Morphotype 74

Figure 72A–C

Description: Fragmentary elytron (part and counterpart) from the Walnut Cove Formation. Medium sized (5.6 mm long, 2.3 mm wide, as preserved), with large punctures covering surface; preservation good, preserved without relief. Asymmetrical, elongate, somewhat rectangular, width subequal throughout preserved portion. Basal margin and apex not preserved; sutural margin straight, lateral margin convex, irregular, possibly artifact of preservation. Very wide lateral rim with single row of rectangular punctures. Punctures large (0.2 mm diameter), rounded or ovate; oriented in at least six rows, rows uneven; distance between punctures greater than puncture diameter. Splotchy, irregular areas of darker pigment present over entire length of elytral surface.

Material: Single specimen, VMNH 97509.

Comments: There are many other Triassic beetles with large elytral punctures, but the shape of this elytron and its arrangement of punctures is unique. Specimen also does not resemble any others from the Solite deposit.

Morphotype 75

Figure 72D–F

Description: Nearly complete elytron (part and counterpart) from the Walnut Cove Formation. Medium sized (6 mm long, 2.2 mm wide), possibly punctate; preservation good, preserved with some relief. Somewhat triangular in shape, length 2.7× width, width subequal in basal half, tapering apically. Basal margin straight, visible corner right-angled, lateral margins slightly convex, apex pointed. Sinuous furrow anterolaterally; thin lateral rim along one margin, long tubular vein along other margin; "schiza" present laterally. Entire surface covered in fine microsculpture, possibly minute punctations; also traces of larger, circular punctation visible anteriorly.

Material: Single specimen, VMNH 97500.

Comments: Elytron belongs to Phoroschizidae (= Schizophoridae; Bouchard and Bosquet, 2020) due to the distinct schiza. The combination of fine microsculpture with traces of larger punctations makes this specimen unique in the Solite deposit.

Morphotype 76

Figure 73A–C

Description: Nearly complete elytron (no counterpart) from the Cow Branch Formation. Medium sized (8.8 mm long, 3.4 mm wide), punctate; preservation good, preserved without relief. Elongate, ovate, length 2.6× width. Basal margin fragmentary, sutural margin straight, lateral margin convex, apex broadly rounded. Thin lateral rim along sutural margin. Punctures small (0.1 mm in diameter), roughly circular, arranged in 10 rows; distance between punctures roughly equal to puncture diameter; punctures not visible near elytral apex.

Material: Single specimen, AMNH 04-87.

Comments: This specimen is relatively large compared to most isolated elytra from the Solite deposit; it does not resemble any other specimens from this deposit.

Morphotype 77

Figure 73D–F

Description: Fragmentary elytron (no counterpart) from the Walnut Cove Formation.

Medium sized (6 mm long, 2.6 mm wide, as preserved), punctate; preservation fair, preserved without relief. Elongate, somewhat ovate, basal margin and majority of one lateral margin not preserved; lateral margins apparently convex, apex obscured. Tubular vein spanning the length of one lateral margin; partial lateral rim visible along other margin. Punctures large (~0.1 mm in diameter) relative to size of elytron, roughly circular, arranged in at least 10 rows; distance between punctures slightly greater than puncture diameter.

Material: Single specimen, VMNH 97571.

Comments: Fragmentary preservation makes comparison difficult, but specimen somewhat resembles elytra of *Lithocupes punctatus* in size (elytra 8.5 mm long, 3.5 mm wide), proportions, and puncture pattern (Carnian, Kyrgyzstan; Ponomarenko, 1969).

Morphotype 78

Figure 74A, B

Description: Almost complete elytron (no counterpart) from the Walnut Cove Formation. Large (15 mm long, 4.4 mm wide, as preserved), punctate; preservation excellent, preserved without relief. Elongate, somewhat symmetrical, length 3.4× width, roughly parallel sided, width subequal in anterior three-quarters. Basal margin rounded with a distinctive notch laterally, corners asymmetrical, lateral margins roughly straight, apex not preserved. Distinct lateral rim; possible tubular veins on both sides of elytron. Punctures small (0.9–0.14 mm diameter), circular, decreasing in size posteriorly; arranged in roughly twenty rows, not present in apical quarter.

Material: Single specimen, VMNH 95456.

Comments: Specimens of this size are unusual in the Solite deposit; the only other beetle with elytra of a similar size is morphotype 61 (figs. 66, 67), though its elytra are not punctate. Specimen belonging to Phoroschizidae (= Schizophoridae; Bouchard and Bosquet, 2020) and closely matching two specimens (PIN, nos. 2470/979 and 2470/897) from the Upper Jurassic Shar Teg lagerstätte of Mongolia (Ponomarenko et al., 2014: fig. 29/3–5), though the sizes of those specimens are unknown.

Morphotype 79

Figure 75A, B

Description: Fragmentary elytron (no counterpart) from the Walnut Cove Formation. Medium sized (9.5 mm long, 3 mm wide, as preserved), punctate; preservation fair, preserved without relief. Elongate, asymmetrical. Basal margin obscured by matrix, lateral margins slightly convex, apex pointed. Lateral rim along one margin. Punctures small, circular to irregularly shaped, arranged in irregular rows, densely covering elytral surface except in apical area.

Material: Single specimen, VMNH 97425.

Comments: Specimen unlike other Solite specimens in both larger size and elytral surface densely covered in somewhat circular punctures.

Morphotype 80

Figure 76A, B

Description: Isolated elytron (no counterpart) from the Walnut Cove Formation. Small (3.3 mm long, 1.2 mm wide, as preserved), with punctate striae; preservation good, preserved with little relief. Ovate, left margin of elytron not preserved. Basal margin apparently straight, visible corner broadly rounded, apex not preserved. No lateral rim; narrow shelf anterolaterally. Ten punctate striae, parallel, not preserved apically; punctures small (~0.04 mm in diameter), rectangular in rightmost three striae, roughly circular in others; distance between punctures much greater than puncture diameter.

Material: Single specimen, VMNH 95483.

Comments: The punctate striae of this specimen are unique in the Solite deposit. An

isolated elytron specimen (*Dzeregia platis*) from the Upper Jurassic Shar Teg lagerstätte of Mongolia (Ponomarenko et al., 2014: fig. 76) shares a somewhat similar pattern of punctate striae, though the Mongolian specimen is slightly larger (5.7 mm long, 2.7 mm wide), and the punctures are not visible on three of the 10 striae. Additionally, the characteristic shortened second stria from the sutural margin of *Dzeregia* is not discernable on the Solite specimen due to its fragmentary lateral preservation.

Morphotype 81

Figure 76C, D

Description: Complete elytron (no counterpart) from the Walnut Cove Formation. Small (2.3 mm long, 1.2 mm wide), striate; preservation good, slightly concave in relief. Symmetrical, length 1.9× width, basal half subequal in width. Basal margin roughly straight, corners obtuse, lateral margins convex, apex broadly rounded. Hinge present anterolaterally. Thin lateral rim along margins. Ten striae, faint, poorly preserved apically; visible only when specimen held at an angle.

Material: Single specimen, VMNH 95443.

Comments: Similar in size and proportions to Solite morphotype 85 (fig. 76K, L) but differs in number of striae, rounded apex, and thinner lateral rim.

Morphotype 82

Figure 76E, F

Description: Isolated elytron (part and counterpart) from the Walnut Cove Formation. Small (2.7 mm long, 1.3 mm wide), striate; preservation good, preserved with exaggerated relief. Almond shaped, length 2.1× width; basal two-thirds subequal in width, tapering apically. Basal margin slightly convex; corners obtuse, rounded; sutural margin straight, lateral margin convex, apex rounded. Thin rim visible laterally and basally. Eight striae, indistinct basally, converging apically.

Material: Illustration and description based on VMNH 96665. Nine additional specimens possibly belonging to this morphotype: VMNH 95034, 96643, 96822, 96825, 97293, 97334, 97561, 97580, and 98470.

Comments: This general shape is fairly common in the Solite deposit, though most specimens have slight differences. Most similar to Solite morphotype 83 (fig. 76G, H) but differs in shape of basal margin.

Morphotype 83

Figure 76G, H

Description: Elytron (no counterpart) from the Walnut Cove Formation. Small (3.3 mm long, 1.8 mm wide), striate; preservation fair, strongly convex in relief. Asymmetrical, length 1.8× width, basal half subequal in width, tapering apically. Basal margin straight, corners poorly preserved, lateral margins convex, apex rounded. Raised lobe oriented parallel to one corner; thin lateral rim along lateral margins. Eight striae, indistinct basally, converging toward apex.

Material: Single specimen, VMNH 96826.

Comments: Somewhat similar in proportions to *Polysitum minutus* elytron (Dunstan, 1923: pl. 3, fig. 25), though Solite specimen is slightly larger and has distinct striae. Most similar to Solite morphotype 82 (fig. 76E, F) but differs in shape of basal margin.

Morphotype 84

Figure 76I, J

Description: Fragmentary elytron (no counterpart) from the Walnut Cove Formation. Small (2.2 mm long, 1.4 mm wide, as preserved) striate; preservation good, convex in relief. Roughly symmetrical in preserved portion. Basal margin and corners not preserved, lateral margins convex, apex pointed. Lateral rim along both mar-

gins, very thin. Ten striae present, well-defined, parallel medially, converging toward apex.

MATERIAL: Single specimen, VMNH 97581.

COMMENTS: Somewhat resembles "*Coleopteron* sp. form E" from Turkey (Laurentiaux, 1946: pl. 3, fig. 8).

Morphotype 85

Figure 76K, L

DESCRIPTION: Complete elytron (no counterpart) from the Cow Branch Formation. Small (2.3 mm long, 1.2 mm wide), striate; preservation good, preserved with slight relief. Near symmetrical, almond shaped, length 1.9× width, basal half subequal in width, tapering apically. Basal margin gently curved; corners asymmetrical, one obtuse and rounded, other roughly right-angled; lateral margins convex, apex pointed. Wide lateral rim along both lateral margins. Nine striae, faint, most visible when specimen viewed at an angle; poorly preserved apically.

MATERIAL: Single specimen, VMNH 54201.

COMMENTS: Similar in size and shape to Solite morphotype 81 (fig. 76C, D), but differs in number of striae, sharply pointed apex, and wider lateral rim.

Morphotype 86

Figure 77A, B

DESCRIPTION: Complete elytron (no counterpart) from the Cow Branch Formation. Small (3.3 mm long, 1.2 mm wide), striate; preservation good, preserved without relief. Elongate, length 2.8× width. Basal margin asymmetrical, outer corner roughly right-angled, inner corner broadly rounded, obtuse; apex broadly rounded. Lateral rim thin, visible along outer margin. Eleven striae, converging both anteriorly and at apex.

MATERIAL: Single specimen, VMNH 50186.

COMMENTS: Only known Solite specimen possessing more than 10 definitive striae.

Morphotype 87

Figure 77C, D

DESCRIPTION: Fragmentary elytron (no counterpart) from the Walnut Cove Formation. Small (3.2 mm long, 1.7 mm wide, as preserved), striate; preservation good, slightly convex in relief. Preserved portion symmetrical. Basal portion not preserved, lateral margins convex, apex broadly rounded. Thin lateral rim; small shelf apically. Eight distinct striae, mostly parallel, converging at apex.

MATERIAL: Single specimen, VMNH 97304.

Morphotype 88

Figure 77E, F

DESCRIPTION: Fragmentary elytron (no counterpart) from the Walnut Cove Formation. Small (1.4 mm long, 0.7 mm wide, as preserved), striate; preservation fair, preserved without relief. Basal portion not preserved, carbon lost but partial stria imprints remain; apex broadly rounded. Lateral rim thin, distinct. Nine well-defined striae, 8th and 9th converge; others do not appear to converge apically.

MATERIAL: Single specimen, VMNH 97376.

COMMENTS: Fragmentary preservation makes comparison to other Solite specimens difficult.

Morphotype 89

Figure 77G, H

DESCRIPTION: Complete elytron (no counterpart) from the Walnut Cove Formation. Small (3.5 mm long, 1.5 mm wide), striate; preservation good, preserved without relief. Elytron asymmetrical, length 2.3× width, basal one-third subequal in width, tapering toward apex. Basal margin straight, small incision medially; corners obtuse, rounded; lateral margins convex, apex pointed. Very thin lateral rim along one lateral margin and half of basal margin. Nine striae, parallel, not preserved basally; curved, bending laterally, not converging at apex.

Material: Single specimen, VMNH 98968.

Comments: This morphotype is most similar to morphotype 90 (3.4 mm long, 1.3 mm wide, as preserved; fig. 77I, J), though apices cannot be compared. Solite morphotypes 51 and 91 (figs. 56, 77K, L) also possess outward curving striae, but morphotype 91 has 10 striae that are much deeper and more pronounced. The elytra of articulated morphotype 51 are also somewhat similar, but have 8 striae and a shelf along the outermost stria.

Morphotype 90

Figure 77I, J

Description: Fragmentary elytron (no counterpart) from the Cow Branch Formation. Small (3.4 mm long, 1.3 mm wide, as preserved), striate; preservation good, preserved without relief. Elongate, asymmetrical, width subequal in anterior two thirds. Basal margin roughly straight, corners obtuse, pointed, apex not preserved. Lateral rim very thin, only visible anterolaterally. Ten striae, parallel, bending laterally.

Material: Single specimen, VMNH 129483.

Comments: Outward-curving striae are similar to those of Solite morphotypes 51, 89, and 91 (figs. 56, 77G, H, 77K, L). Specimen is most similar in size and shape to morphotype 89 (3.5 mm long, 1.5 mm wide), though elytral apices cannot be compared. Morphotype 91 also has striae that curve similarly, but it has 10 striae and they are deeper and more pronounced. The elytra of articulated morphotype 51 are also somewhat similar, but possess eight striae and a shelf along the outermost stria.

Morphotype 91

Figure 77K, L

Description: Fragmentary elytron (part and counterpart) from the Walnut Cove Formation. Small (2.7 mm long, 1.3 mm wide, as preserved), striate; preservation poor, carbon lost anteriorly but stria impressions remain; preserved with relief. Somewhat ovate in shape. Basal margin and apex not preserved, widest medially; lateral margins convex. Thin lateral rim present along one margin. Ten striae, very deep, distinct; bend laterally as approach apex.

Material: Single specimen, VMNH 97346.

Comments: Striae are deep and pronounced like those of *Ischichucasyne santajuanaensis* (Gallego et al., 2005: pl. 3, fig. 7). Striae curve in a similar way to those of Solite morphotypes 51, 89, and 90 (figs. 56, 77G, H, 77I, J).

Morphotype 92

Figure 78A, B

Description: Complete elytron (no counterpart) from the Walnut Cove Formation. Small (2.7 mm long, 1 mm wide), striate; preservation good, preserved without relief. Asymmetrical, somewhat almond shaped, elongate, length 2.7× width, widest medially. Basal margin convex, preserved corner obtuse; sutural margin roughly straight, apex pointed. Lateral rim thin, visible along almost entire elytron. Possibly eight striae, only four distinct; striae very faint, preserved only medially.

Material: Single specimen, VMNH 95536.

Comments: Similar in size and proportions to isolated elytron specimens assigned to the genus *Ademosyne,* e.g., *Ademosyne punctuada* (2.8–4.5 mm long, 1.2–1.7 mm wide; 6–9 striae) from the Carnian of Argentina (Martins-Neto et al., 2006).

Morphotype 93

Figure 78C, D

Description: Elytron (part and counterpart) from the Walnut Cove Formation. Small (3 mm long, 1.1 mm wide), striate; preservation good, preserved with some relief. Ovate, symmetrical, length 2.7× width, widest medially, tapering strongly in apical third. Basal and lateral margins strongly convex, apex obscured by matrix. Lateral rim distinct, thin, present along both

margins. Nine striae, faint, poorly preserved, converging basally and apically.

MATERIAL: Single specimen, VMNH 97305.

COMMENTS: Counterpart to VMNH 96828. Similar in proportions and striae configuration (9–10 striae converging apically) to "Species 7" of Papier et al. (2005) from the Anisian of France, though the French specimen is much larger (9 mm long, 3 mm wide). Does not resemble any other Solite specimens.

Morphotype 94

Figure 78E, F

DESCRIPTION: Complete elytron (part and counterpart) from the Walnut Cove Formation. Small (3 mm long, 1 mm wide), striate; preservation good, preserved without relief. Elongate, asymmetrical, distinctly narrow; length 3× width, widest point roughly one-third the length from basal margin, tapering apically. Basal margin strongly convex, lateral margins roughly straight, apex pointed. Slight ridge anterolaterally; lateral rim thin, distinct, present along both lateral margins. Seven distinct striae, faint, converging apically.

MATERIAL: Illustration and description based on VMNH 97583. One additional specimen possibly belonging to this morphotype: VMNH 99324.

COMMENTS: Similar in size and proportions to Solite specimen VMNH 99324. Also similar in proportions to *Tryoniopsis granulata* (Dunstan, 1923: pl. 7, fig. 59) from the Denmark Hill insect bed of Queensland, Australia, though the Australian specimen is larger (5.7 mm long, 1.8 mm wide) and has nine striae.

Morphotype 95

Figure 78G, H

DESCRIPTION: Isolated elytron (no counterpart) from the Walnut Cove Formation. Small (3.5 mm long, 0.9 mm wide), striate; preservation fair, preserved without relief. Elongate, very narrow, length 3.9× width, tapering apically; widest point roughly one-third the length from basal margin. Basal margin partially preserved, convex; apex narrow, pointed. Very thin rim along both lateral margins. Striae faint, poorly preserved, at least four visible; parallel, not converging.

MATERIAL: Single specimen, VMNH 98277.

COMMENTS: Specimen is distinctly narrow; does not resemble any other elytron specimens from the Solite deposit.

Morphotype 96

Figure 78I, J

DESCRIPTION: Elytron (no counterpart) from the Cow Branch Formation. Small (2.3 mm long, 0.7 mm wide, as preserved), striate; preservation fair, preserved without relief. Specimen very faint, not visible without use of ethanol. Distinctively narrow, length >3.3× width, widest medially. Basal margin and corners poorly preserved, lateral margins slightly convex, apex not visible. No lateral rim. Eight striae visible, faint, preserved only in central portion.

MATERIAL: Single specimen, VMNH 95971.

COMMENTS: Specimen very faint, near invisible without using ethanol.

Morphotype 97

Figure 78K, L

DESCRIPTION: Isolated elytron (part and counterpart) from the Walnut Cove Formation. Medium sized (7.5 mm long, 2.7 mm wide, as preserved), striate; preservation good, preserved with slight relief. Oblong, narrowest basally, width subequal throughout majority of preserved portion. Basal margin not preserved, lateral margins roughly straight, apex obscured by matrix. Thin lateral rim. Ten well-defined striae, straight, parallel, not converging, oriented at an angle relative to lateral margins.

MATERIAL: Single specimen, VMNH 96824.

COMMENTS: Counterpart to specimen VMNH 95508. Specimen is fairly large for the Solite material. Does not resemble any other specimen from the Solite deposit.

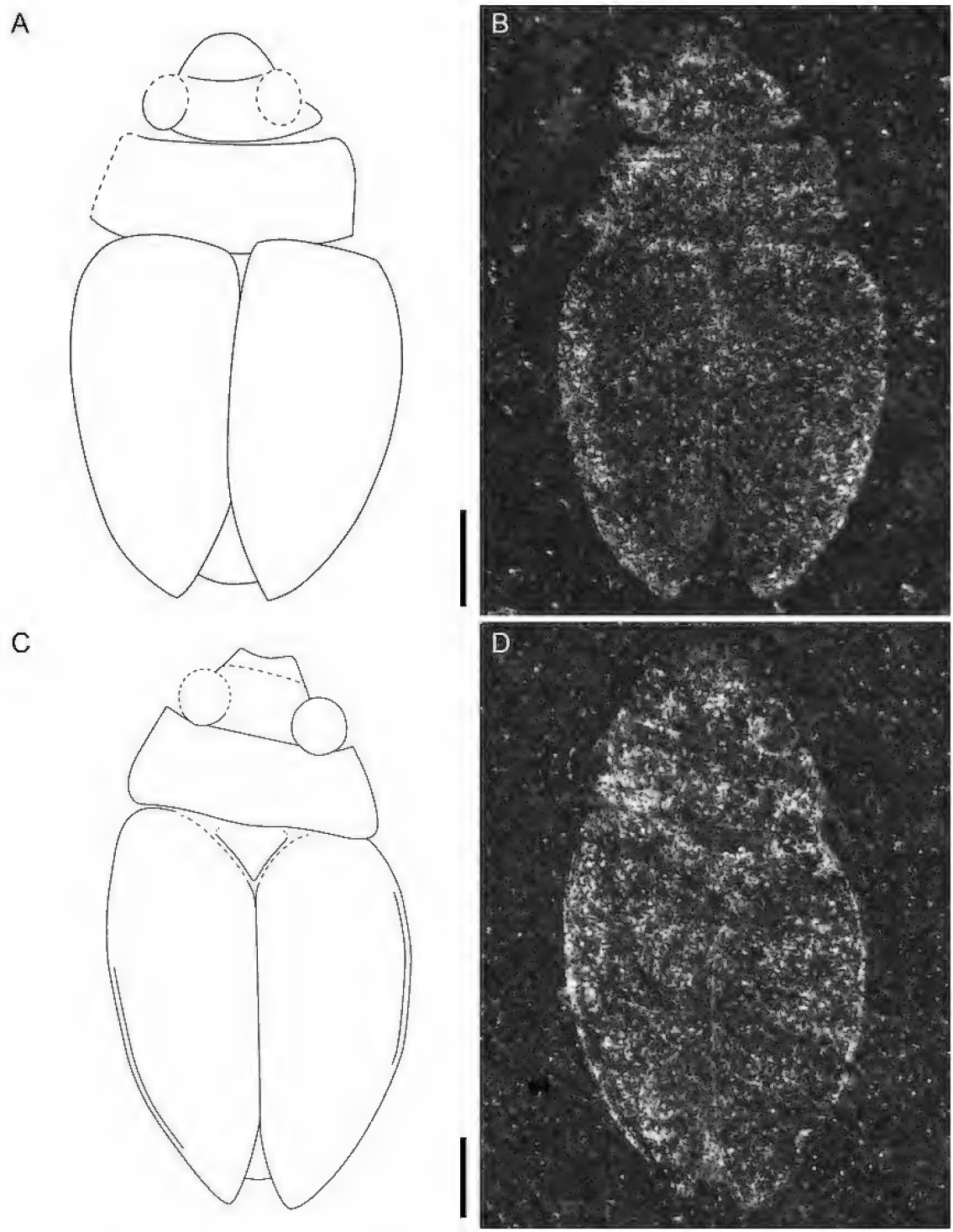

FIG. 5. Morphotypes 1 and 2. **A, B.** Morphotype 1, VMNH 95900. **C, D.** Morphotype 2, YPM IP 036448. Scale bars: 0.5 mm.

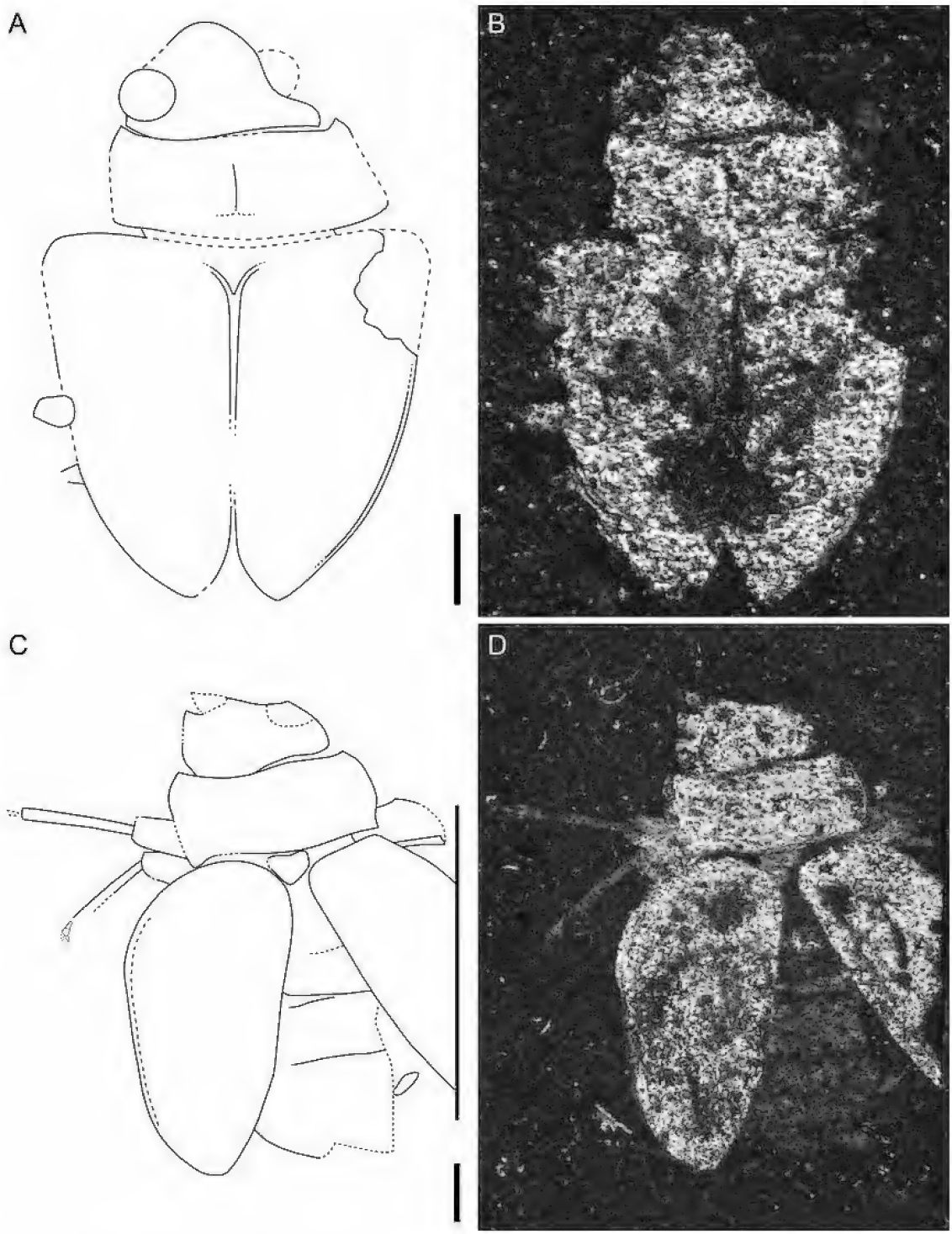

FIG. 6. Morphotypes 3 and 4. **A, B.** Morphotype 3, AMNH 04-93. **C, D.** Morphotype 4, VMNH 129480. Scale bars: 0.5 mm.

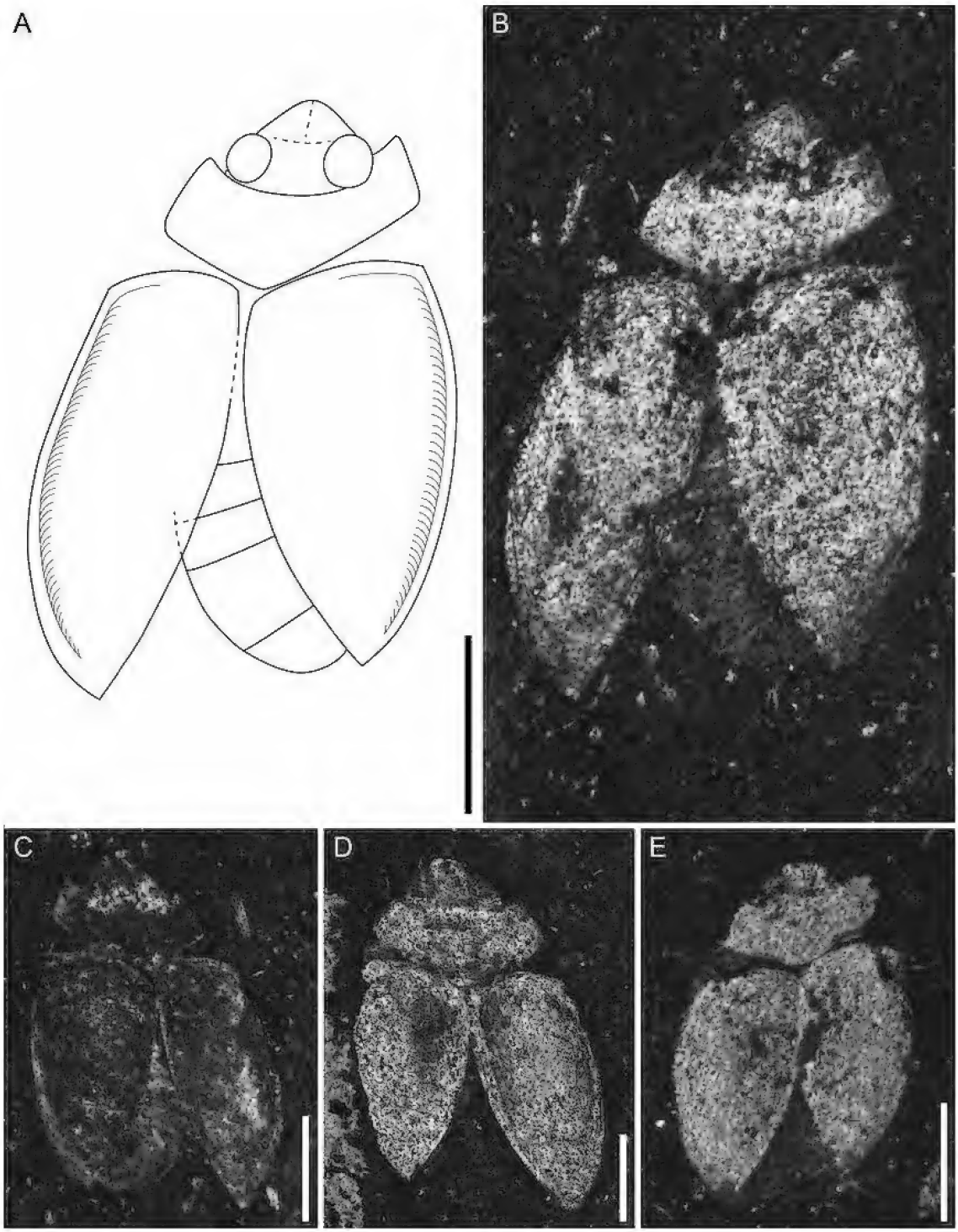

FIG. 7. Morphotype 5. **A–C.** VMNH 95086. **D.** YPM IP 034686, photograph courtesy of YPMNH. **E.** VMNH 94862, photograph courtesy of VMNH. Scale bars: 1 mm.

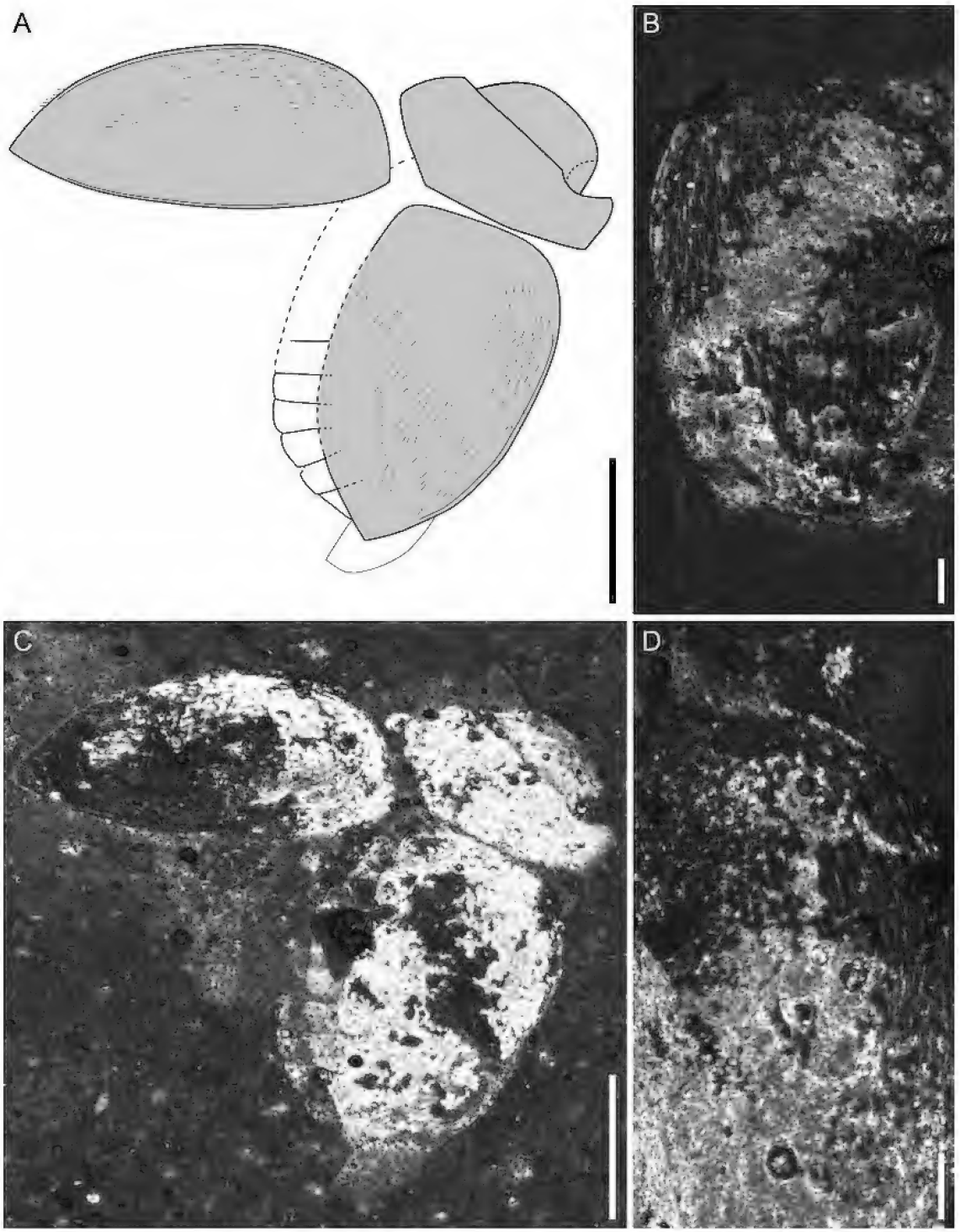

FIG. 8. Morphotype 6, VMNH 53853. **A, C.** Part. **B, D.** Counterpart, elytral setae. Scale bars: A, C: 0.5 mm; B, D: 0.1 mm.

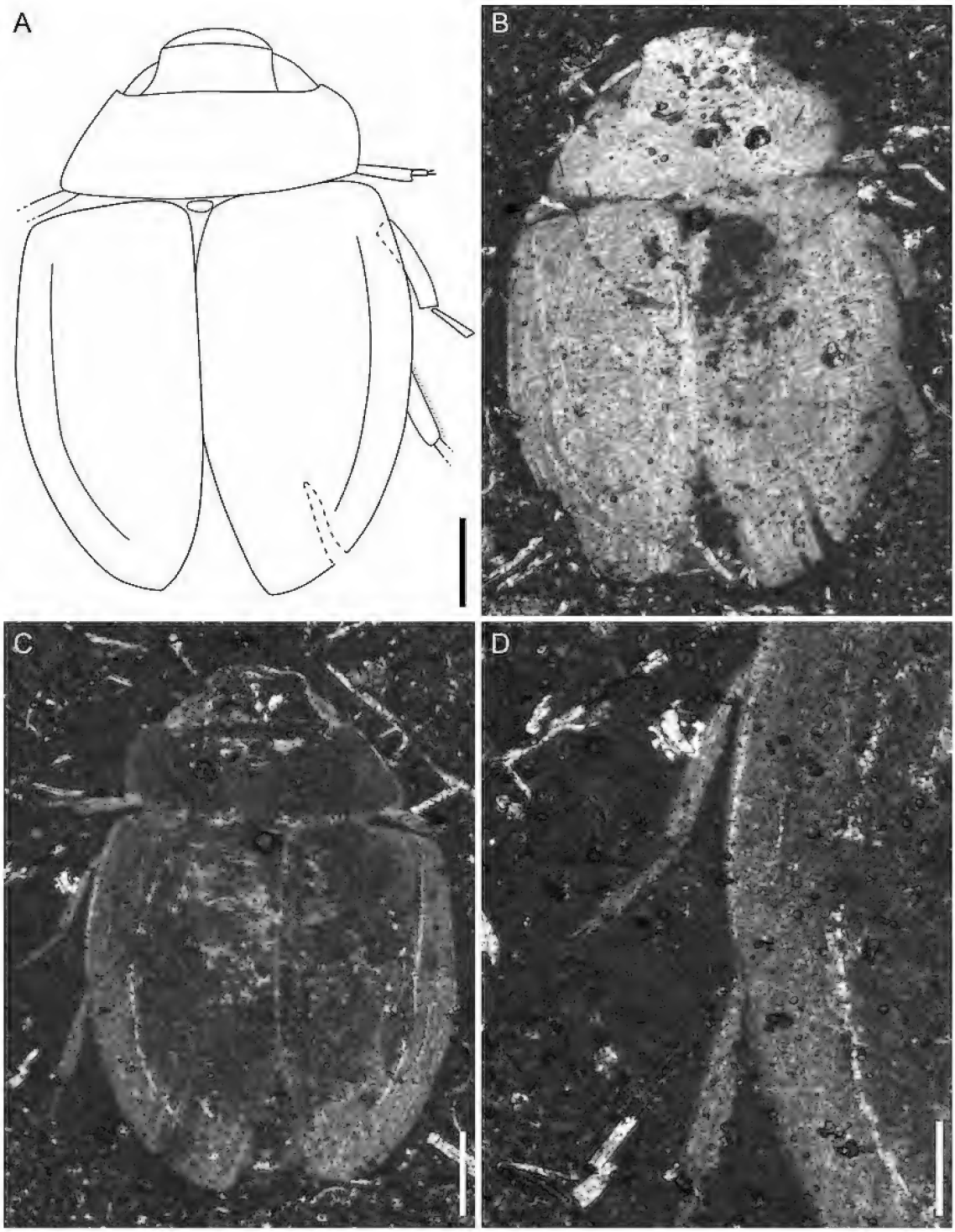

FIG. 9. Morphotype 7, VMNH 90298. **A, B.** Part. **C.** Counterpart. **D.** Counterpart, middle leg and hind leg showing fine setae. Scale bars: A–C: 0.5 mm; D: 0.25 mm.

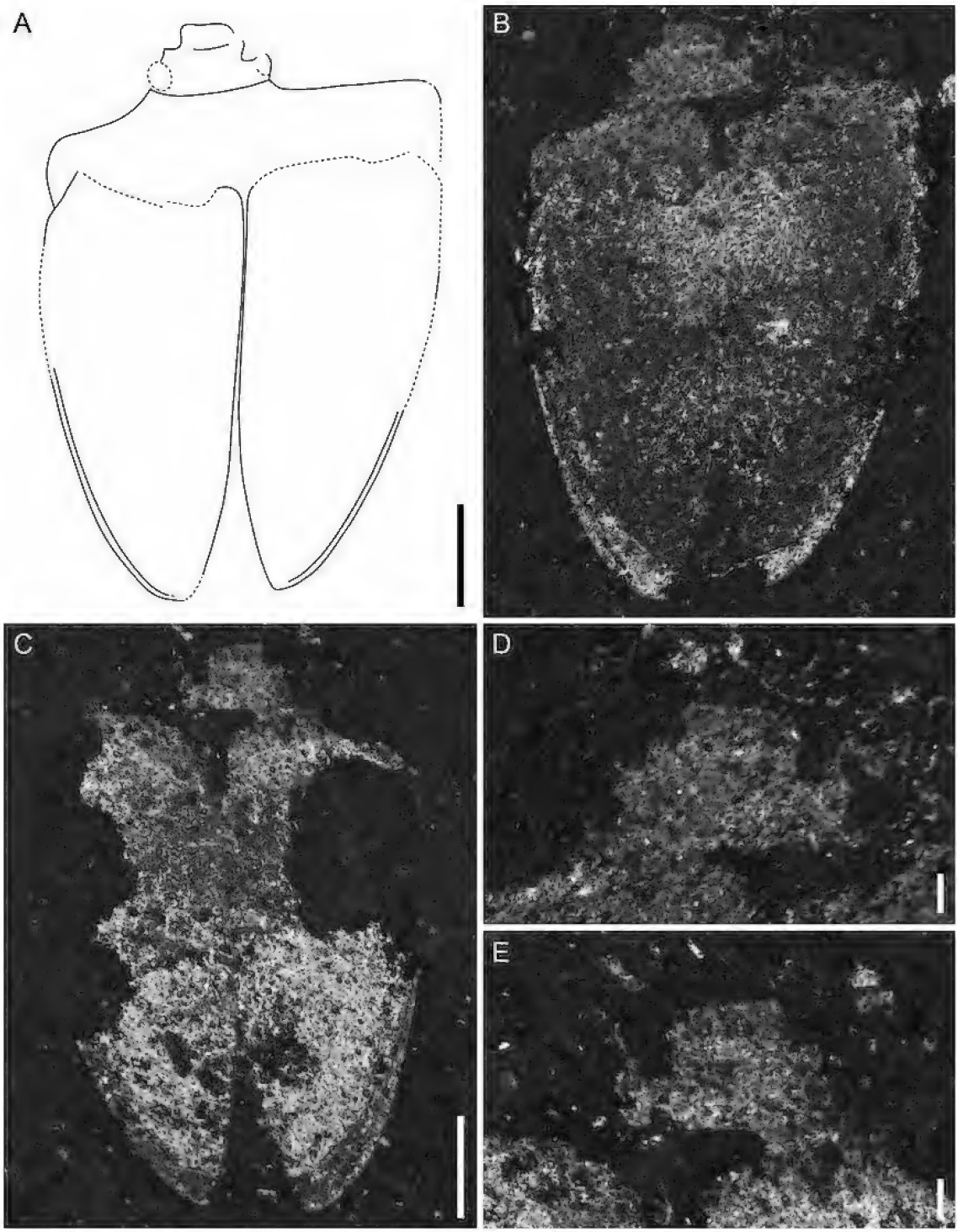

FIG. 10. Morphotype 8, AMNH 04-90. **A, B.** Part. **C.** Counterpart. **D.** Head of part. **E.** Head of counterpart. Scale bars: A–C: 0.5 mm; D, E: 0.1 mm.

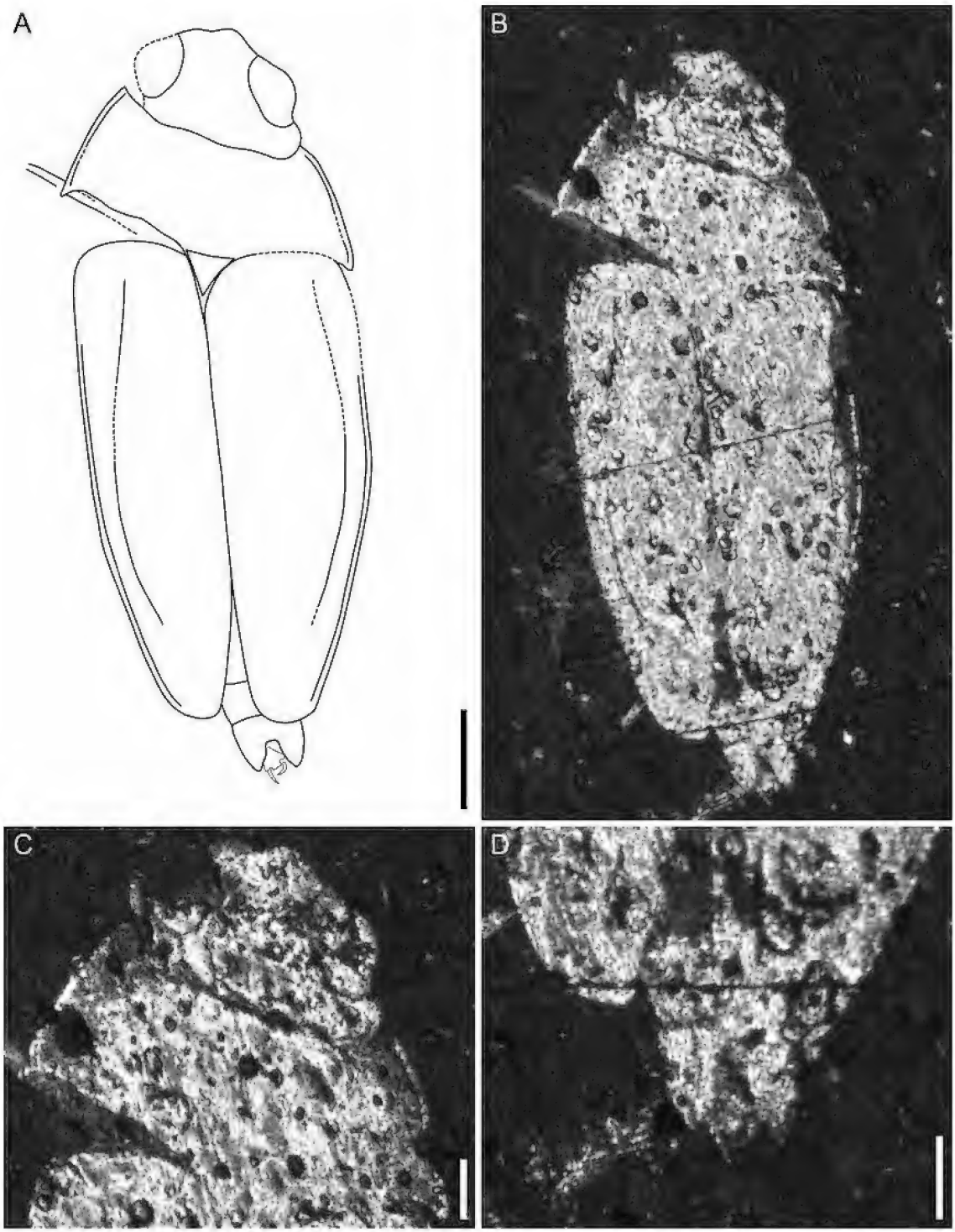

FIG. 11. Morphotype 9, AMNH 04-77. **A, B.** Habitus. **C.** Head and pronotum. **D.** Tip of abdomen showing partial genitalia. Scale bars: A–C: 0.5 mm; D: 0.1 mm.

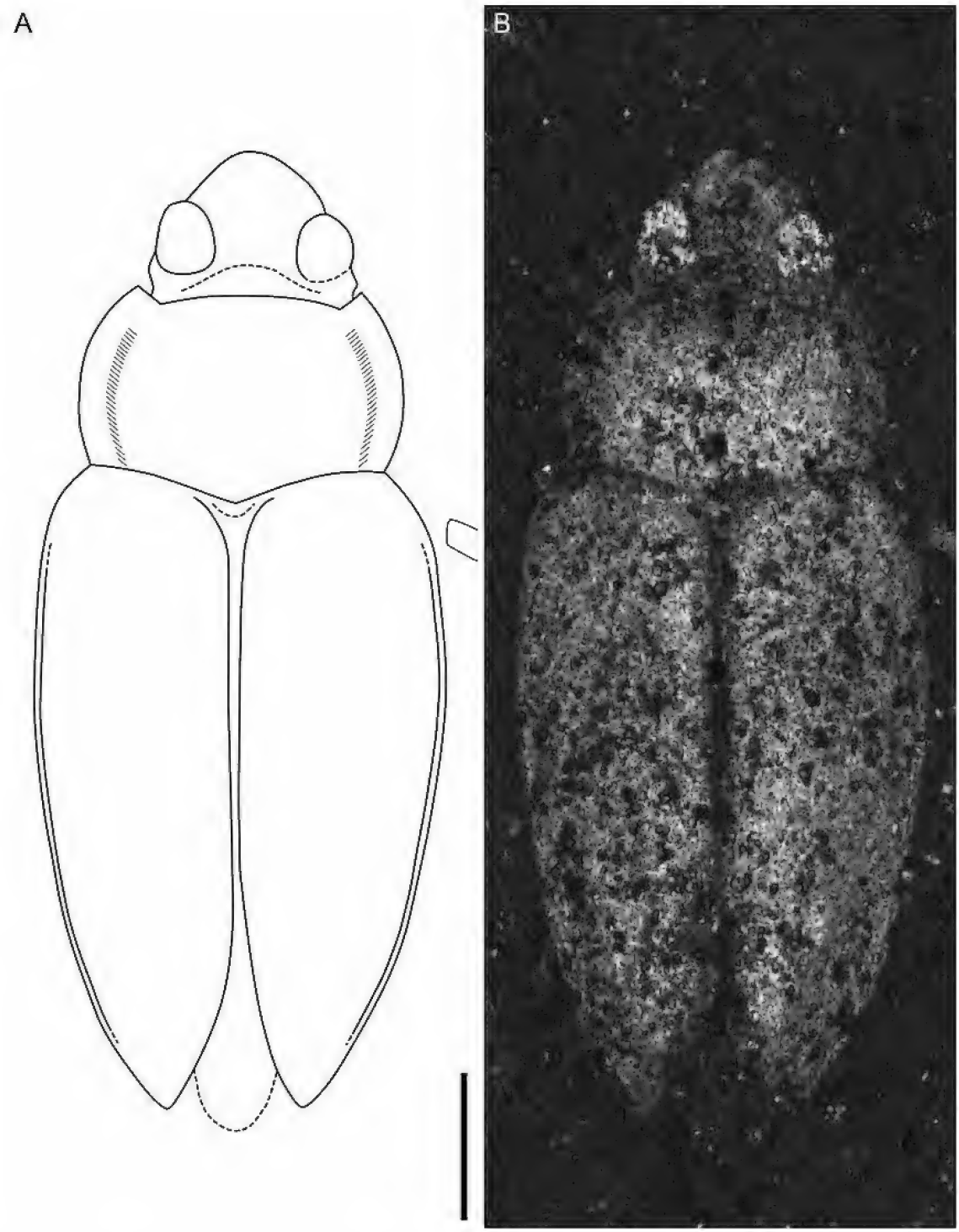

FIG. 12. Morphotype 10, AMNH 04-88. Scale bar: 0.5 mm.

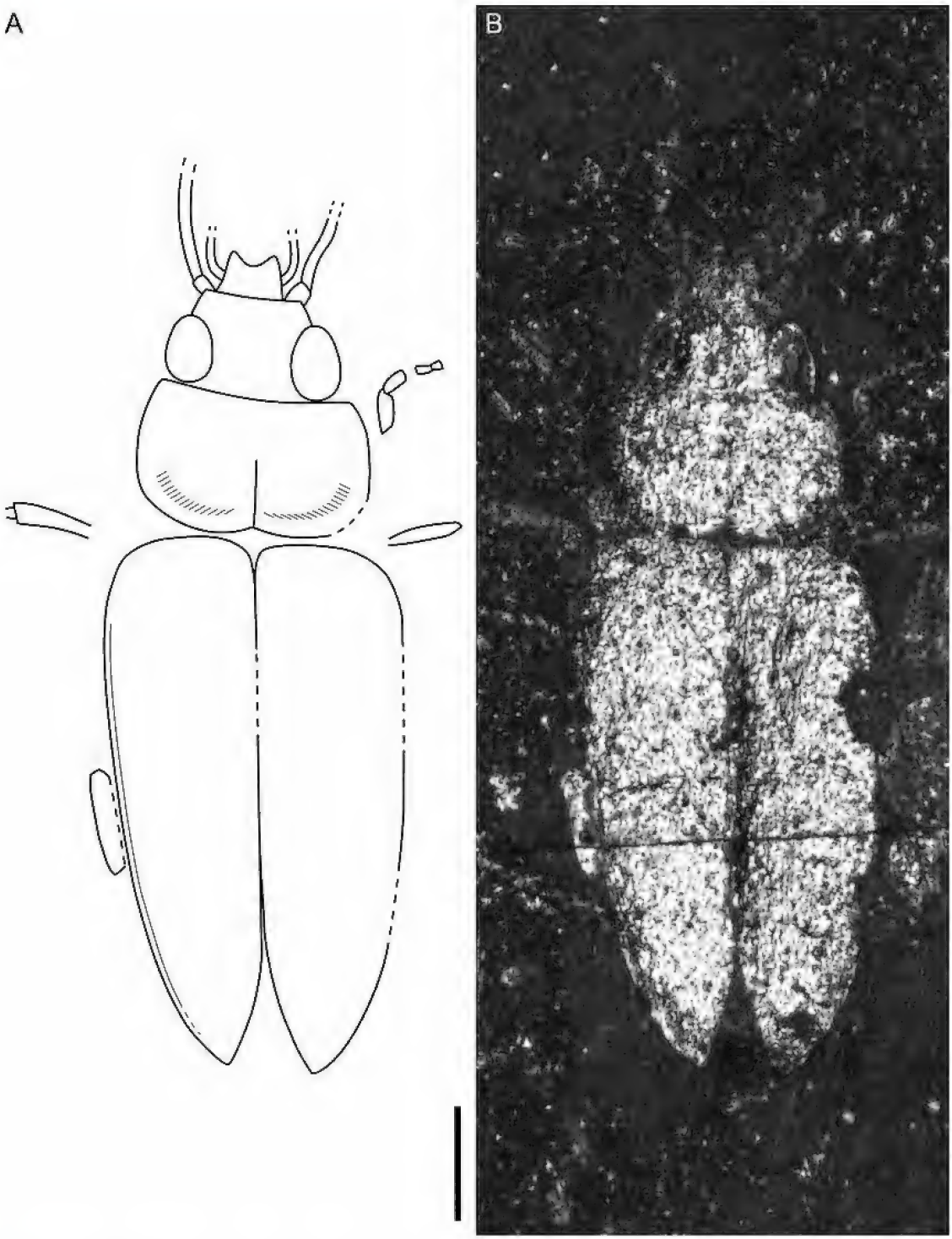

FIG. 13. Morphotype 11, VMNH 51912. Scale bar: 0.5 mm.

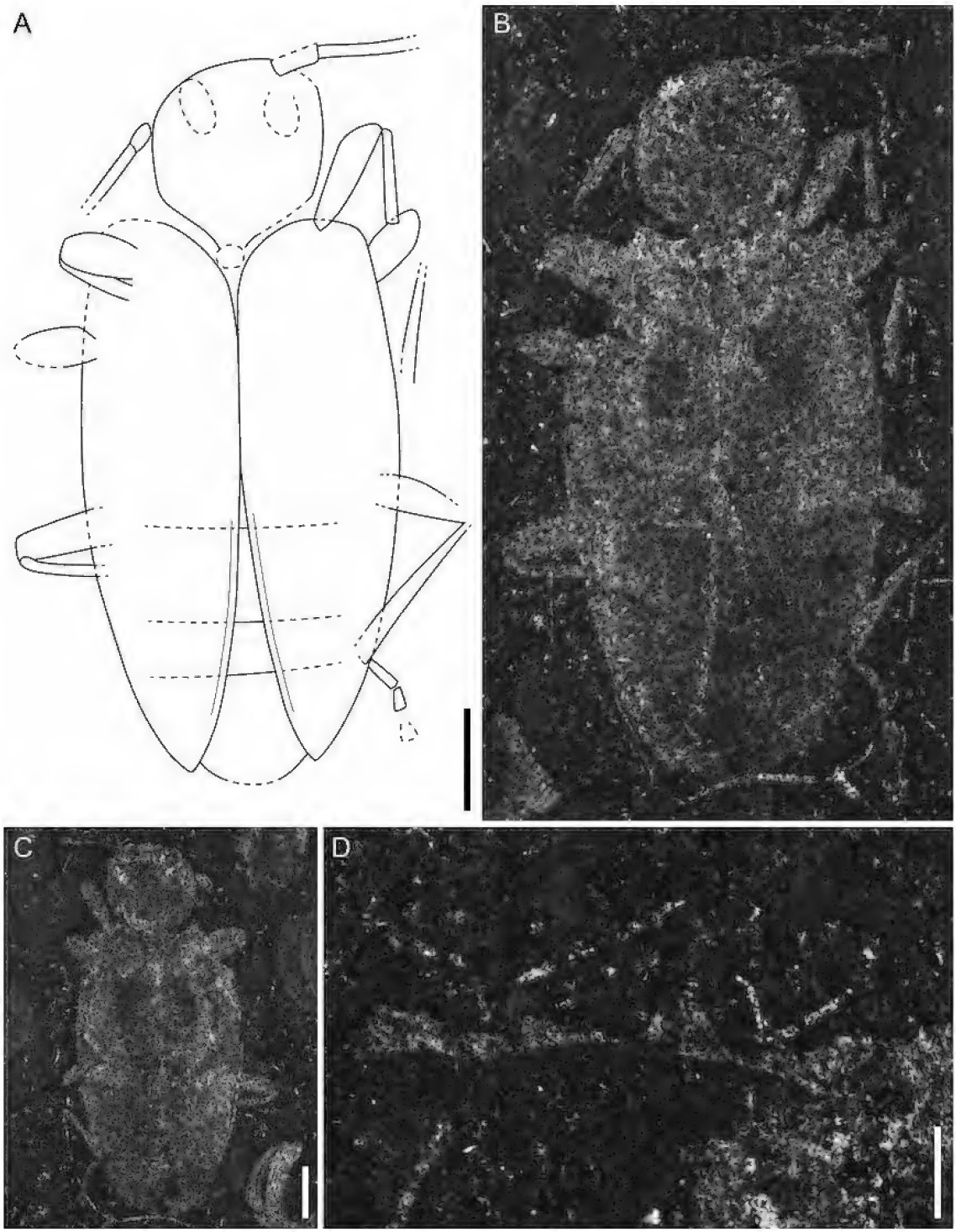

FIG. 14. Morphotype 12, VMNH 51273. **A, B.** Part. **C.** Counterpart. **D.** Antenna of counterpart. Scale bars: A–C: 1 mm; D: 0.25 mm.

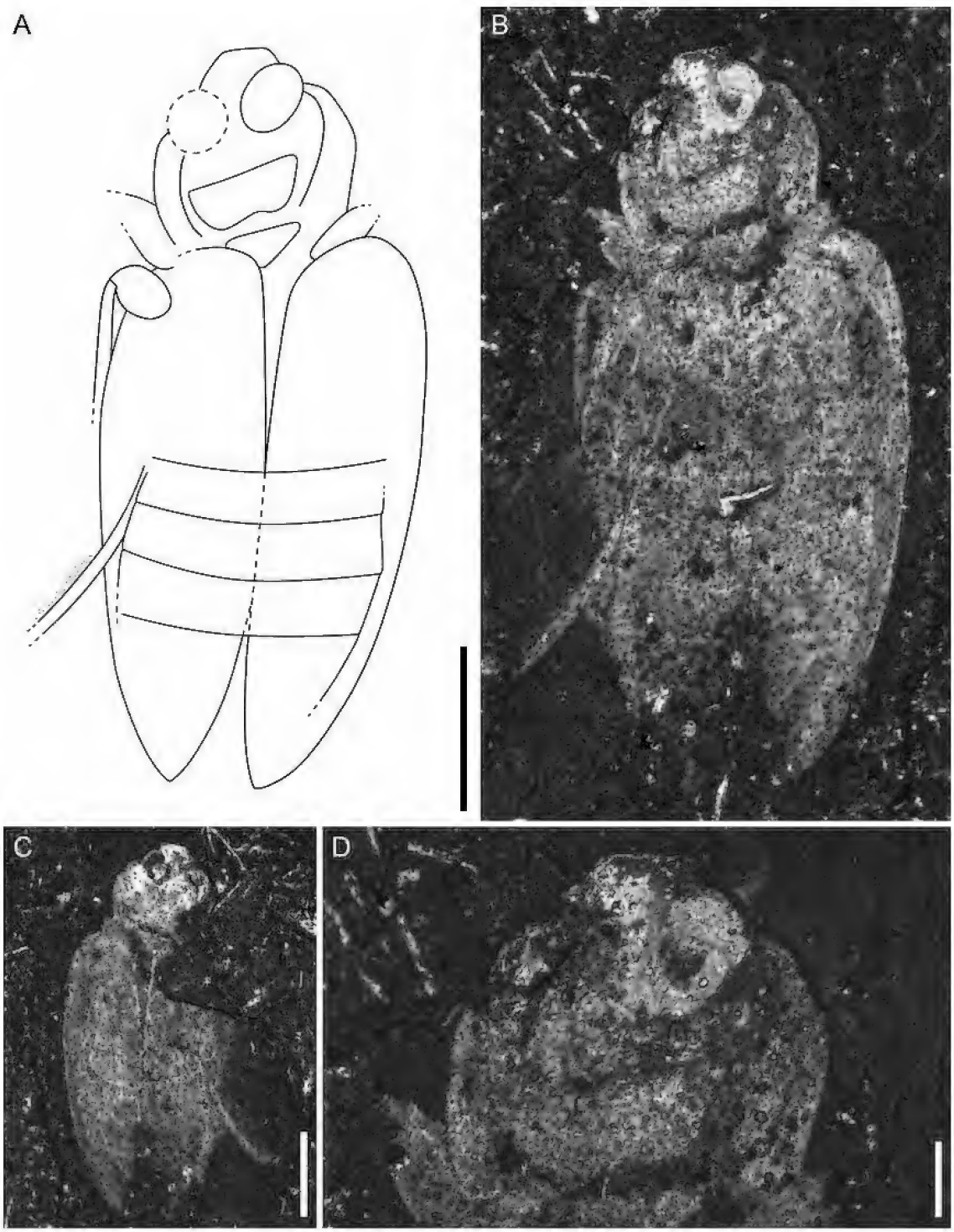

FIG. 15. Morphotype 13, VMNH 51271. **A, B.** Part. **C.** Counterpart. **D.** Head of part. Scale bars: A–C: 1 mm; D: 0.25 mm.

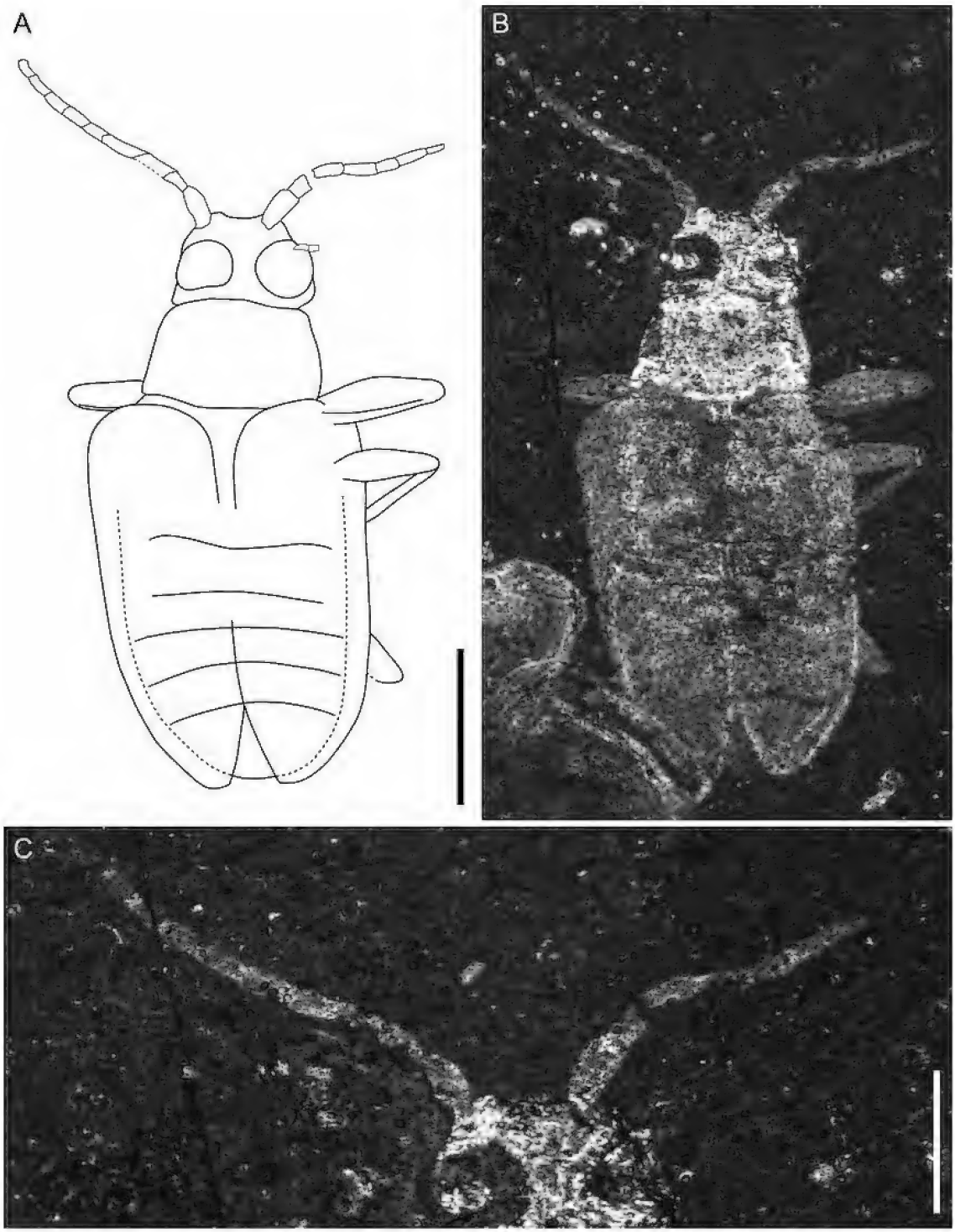

FIG. 16. Morphotype 14, VMNH 51944. **A, B.** Habitus. **C.** Antennae. Scale bars: A, B: 1 mm; C: 0.5 mm.

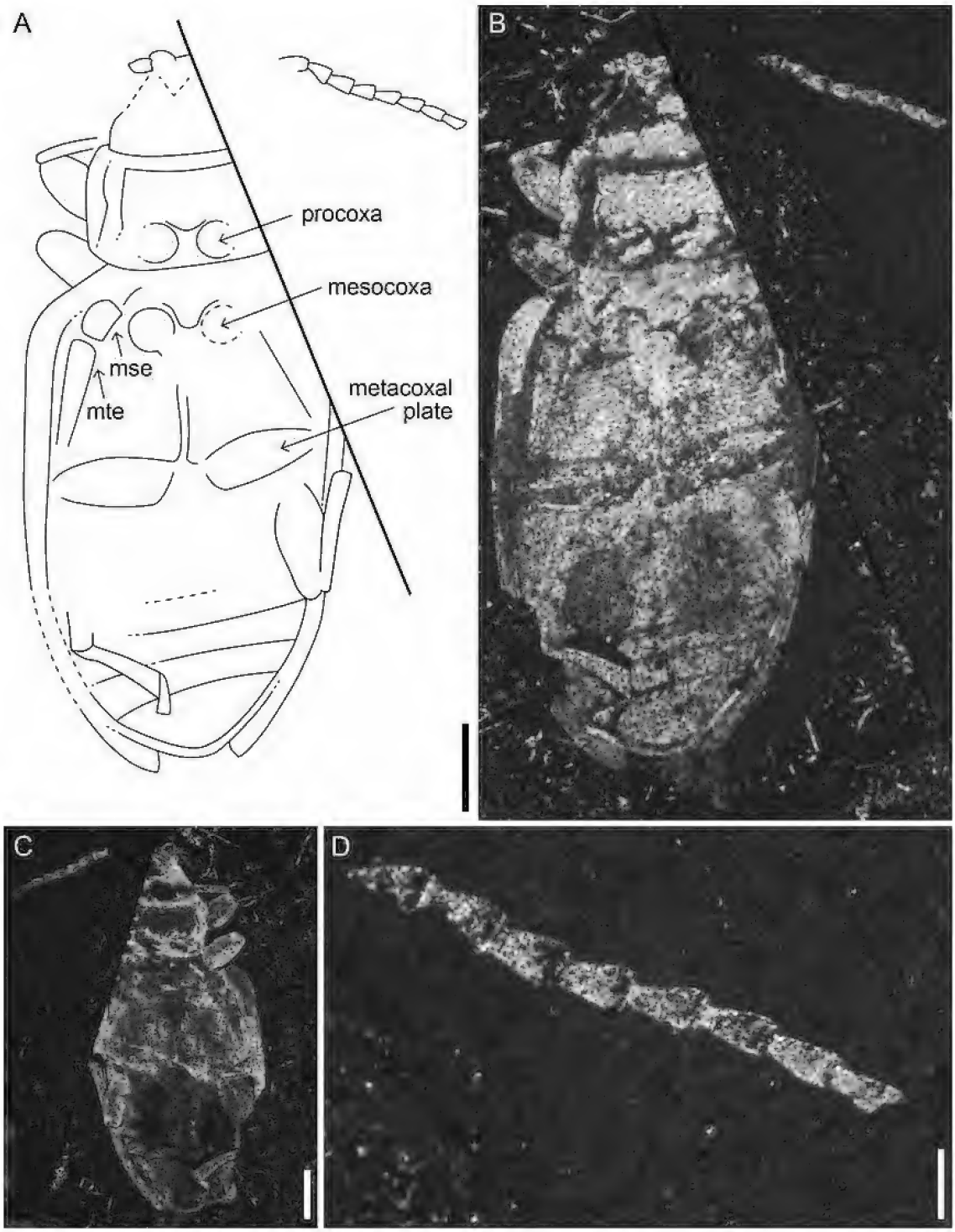

FIG. 17. Morphotype 15, VMNH 51991. **A, B.** Part. **C.** Counterpart. **D.** Antenna of part. **mse** = mesepimeron; **mte** = metepisternum. Scale bars: A–C: 1 mm; D: 0.25 mm.

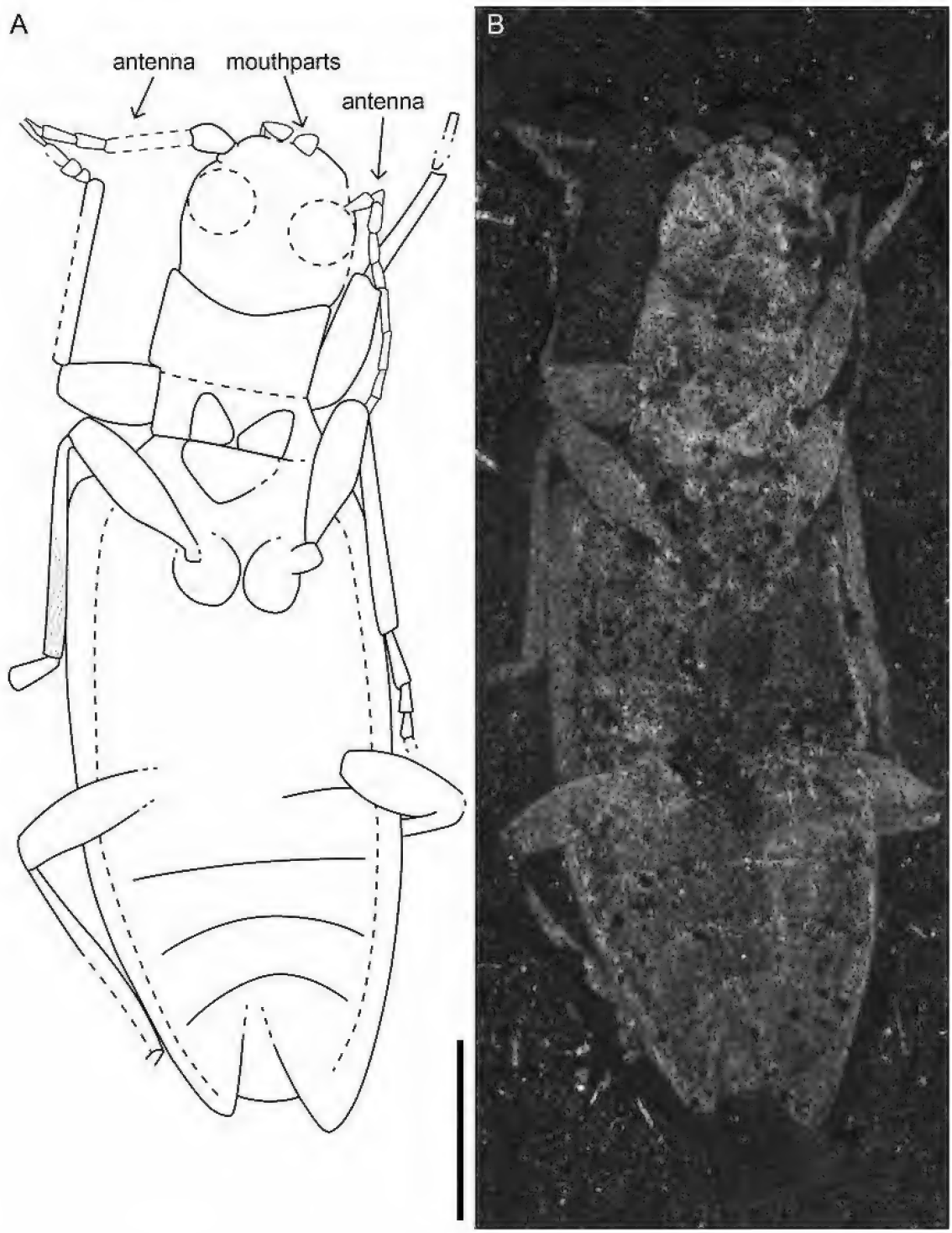

FIG. 18. Morphotype 16, VMNH 211462. Scale bar: 1 mm.

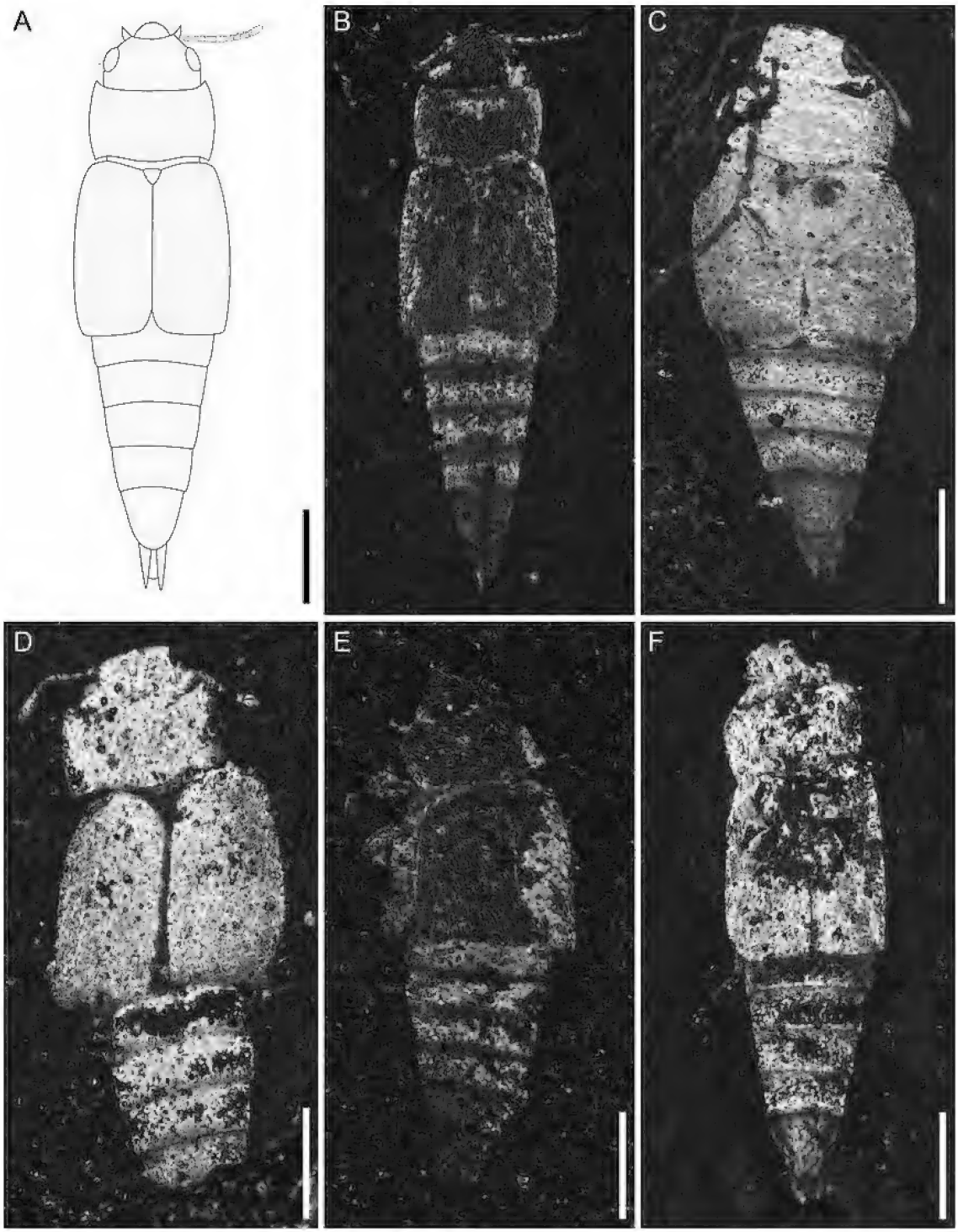

FIG. 19. *Leehermania prorova*. **A, B.** VMNH 49570 (holotype, formerly published as VMNH 734, Chatzimanolis et al., 2012). **C.** VMNH 50174. **D.** VMNH 50277. **E.** VMNH 50064. **F.** YPM IP 036452, staphylinid possibly belonging to *L. prorova*. Scale bars: 0.5 mm.

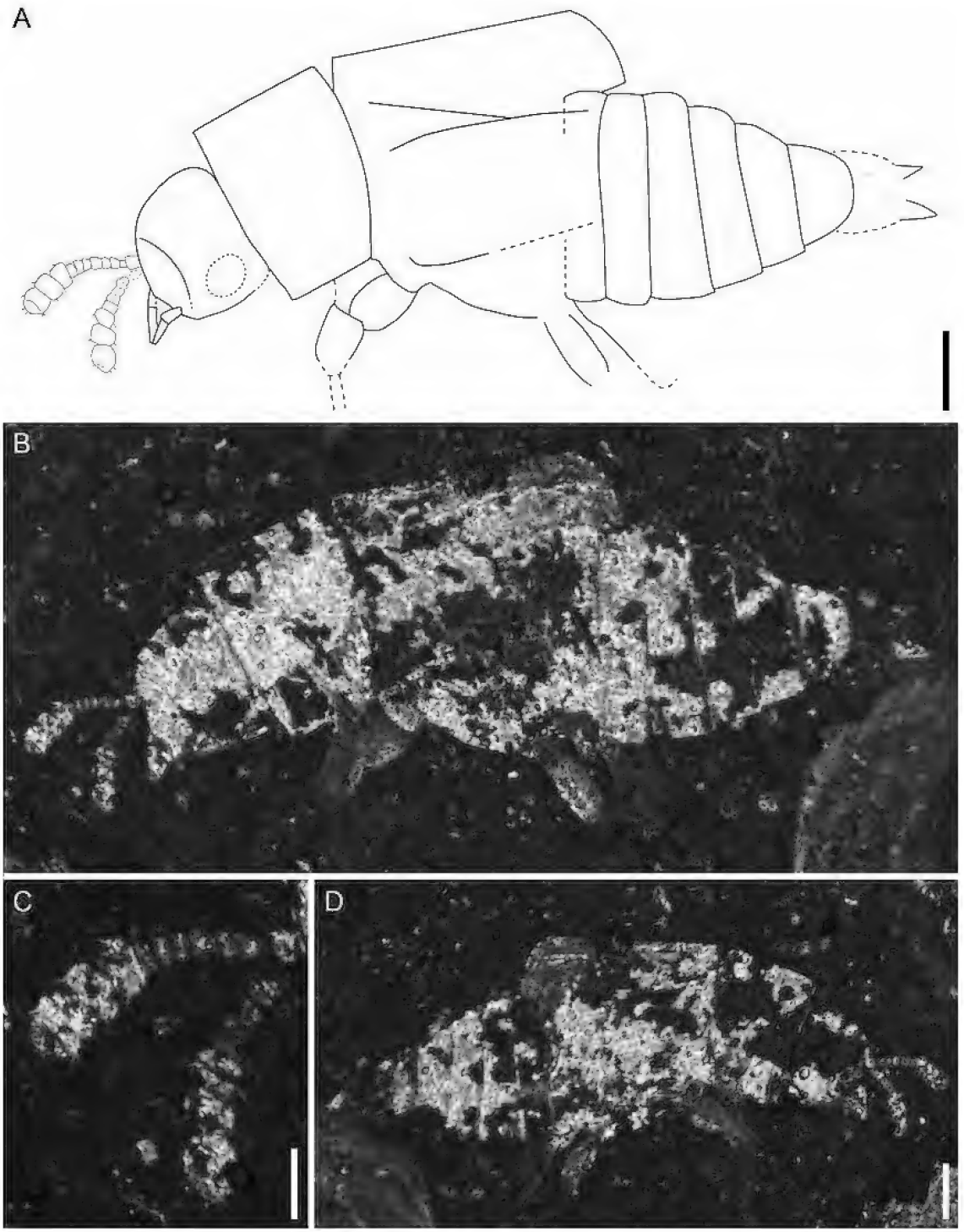

FIG. 20. Morphotype 17, VMNH 50075. **A, B.** Part. **C.** Antennae of part showing fine setae. **D.** Counterpart. Scale bars: A, B, D: 0.25 mm; C: 0.1 mm.

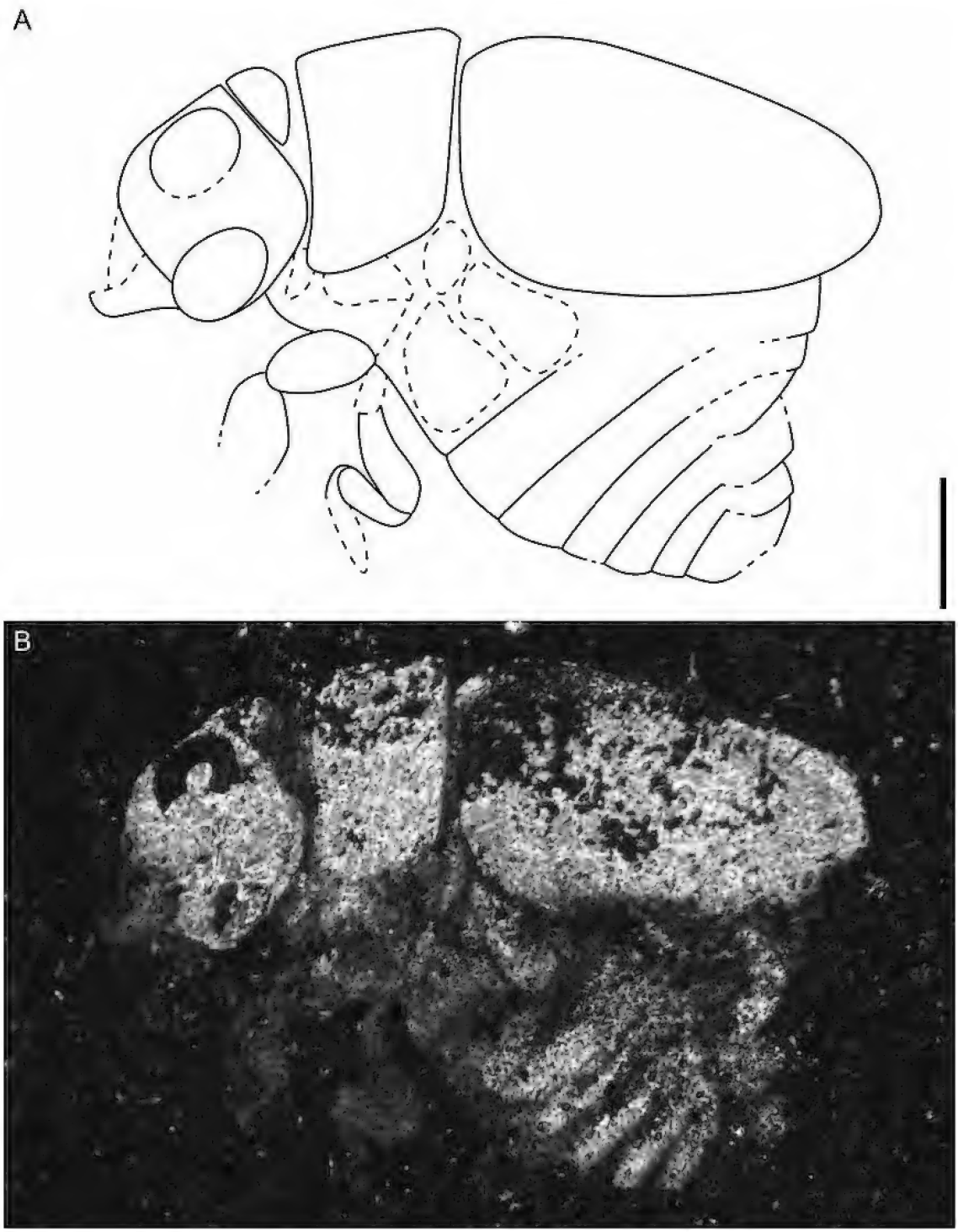

FIG. 21. Morphotype 18, VMNH 95059. Scale bar: 0.5 mm.

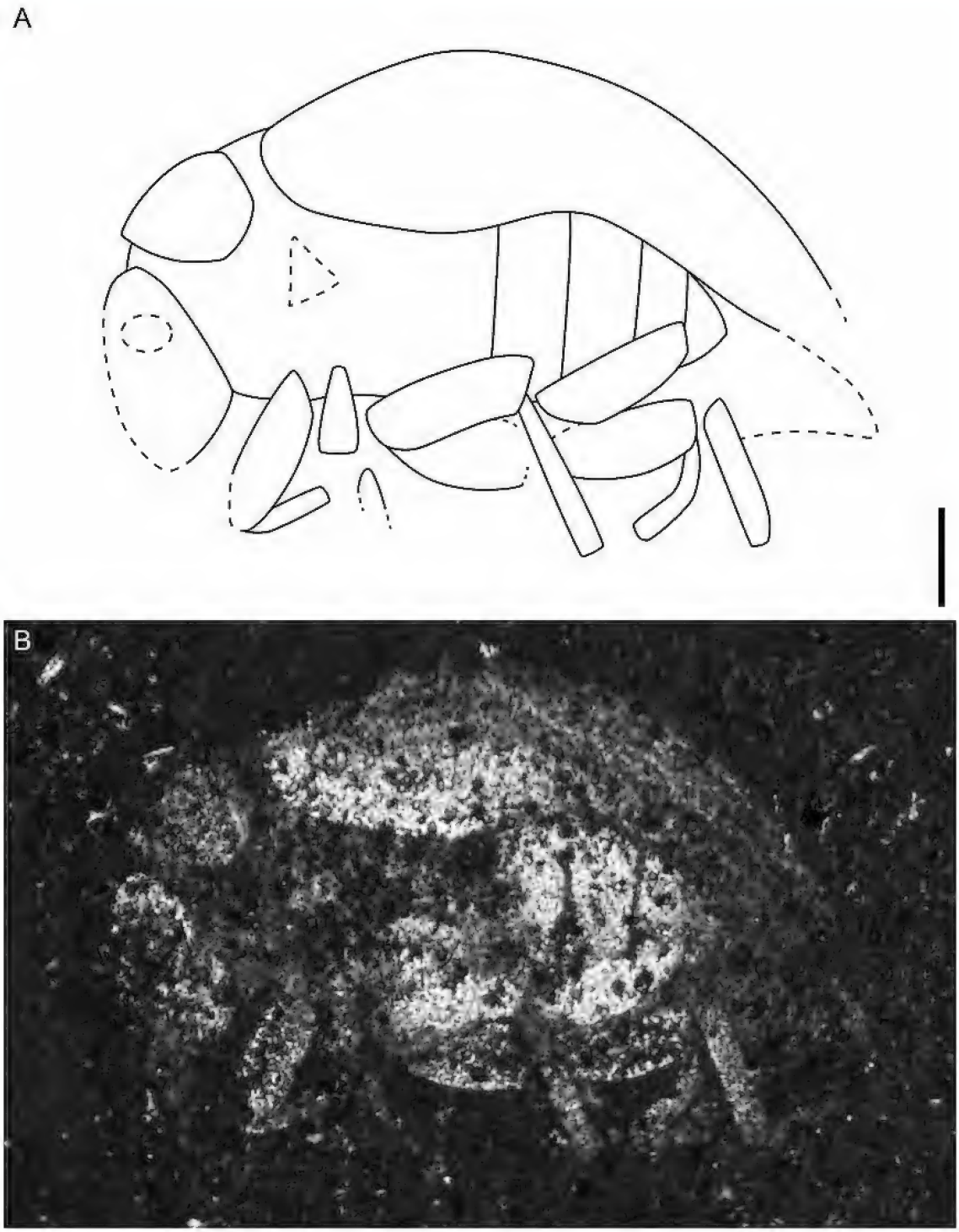

FIG. 22. Morphotype 19, VMNH 94513. Scale bar: 0.25 mm.

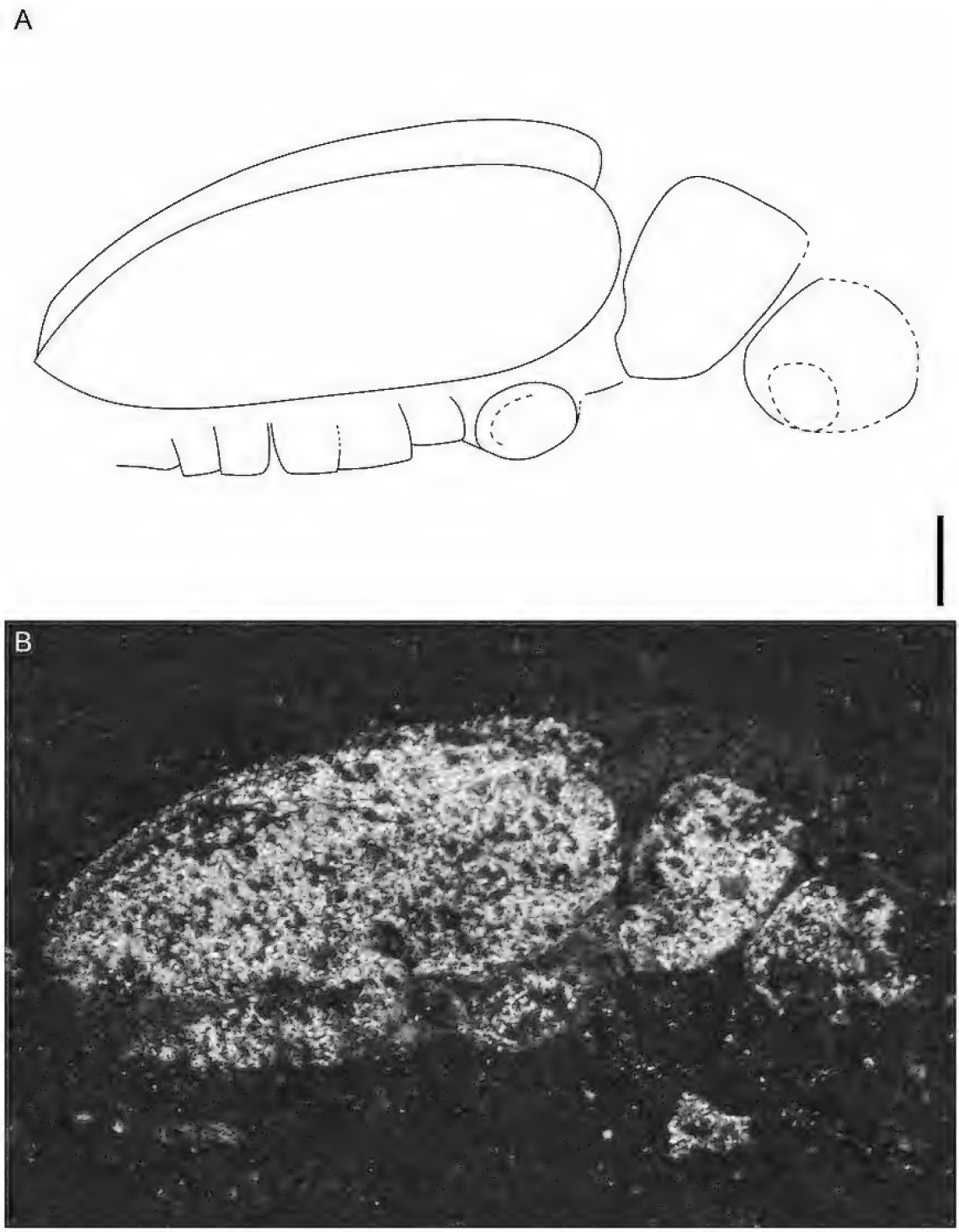

FIG. 23. Morphotype 20, YPM IP 036445. Scale bar: 0.25 mm.

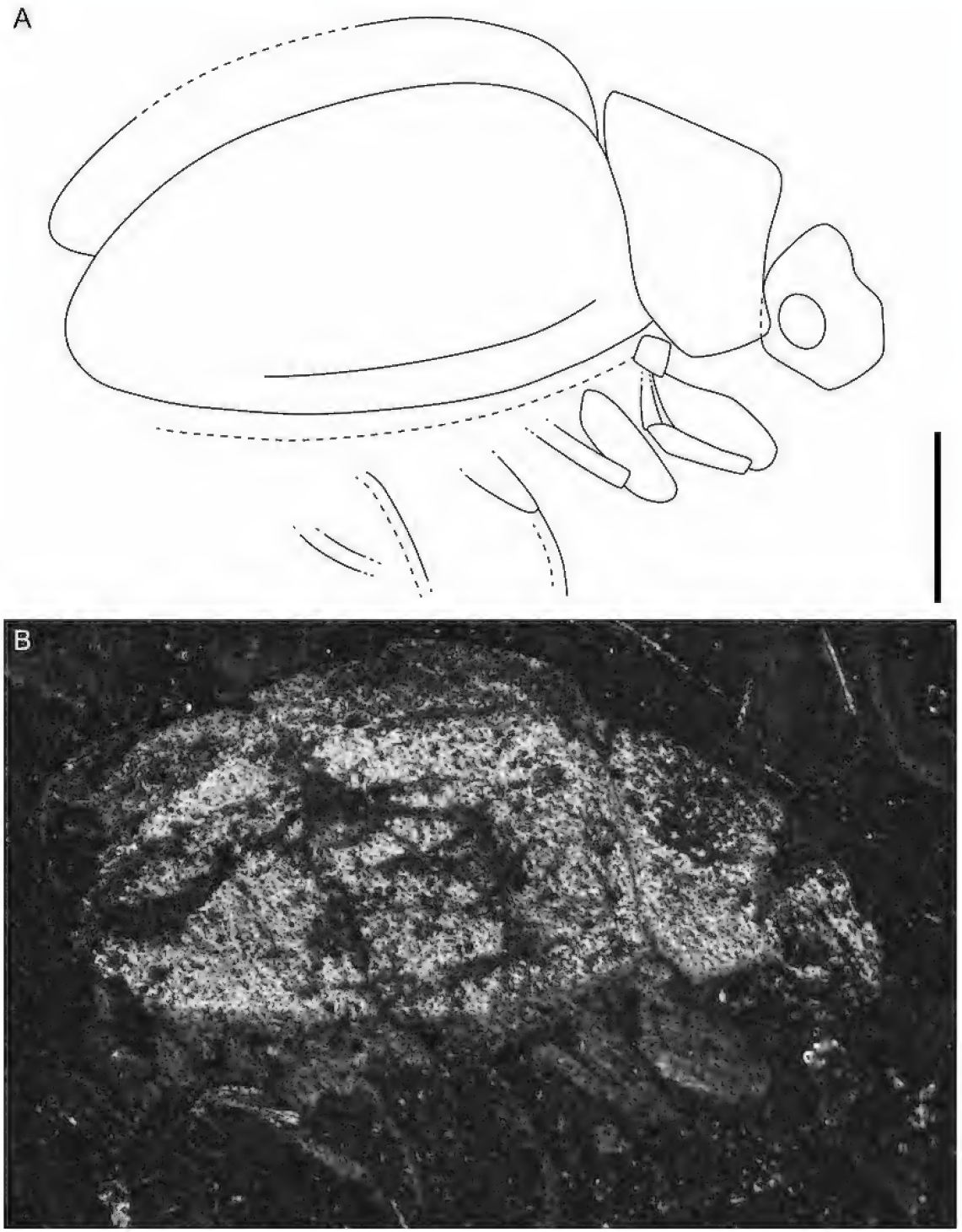

FIG. 24. Morphotype 21, VMNH 51491. Scale bar: 1 mm.

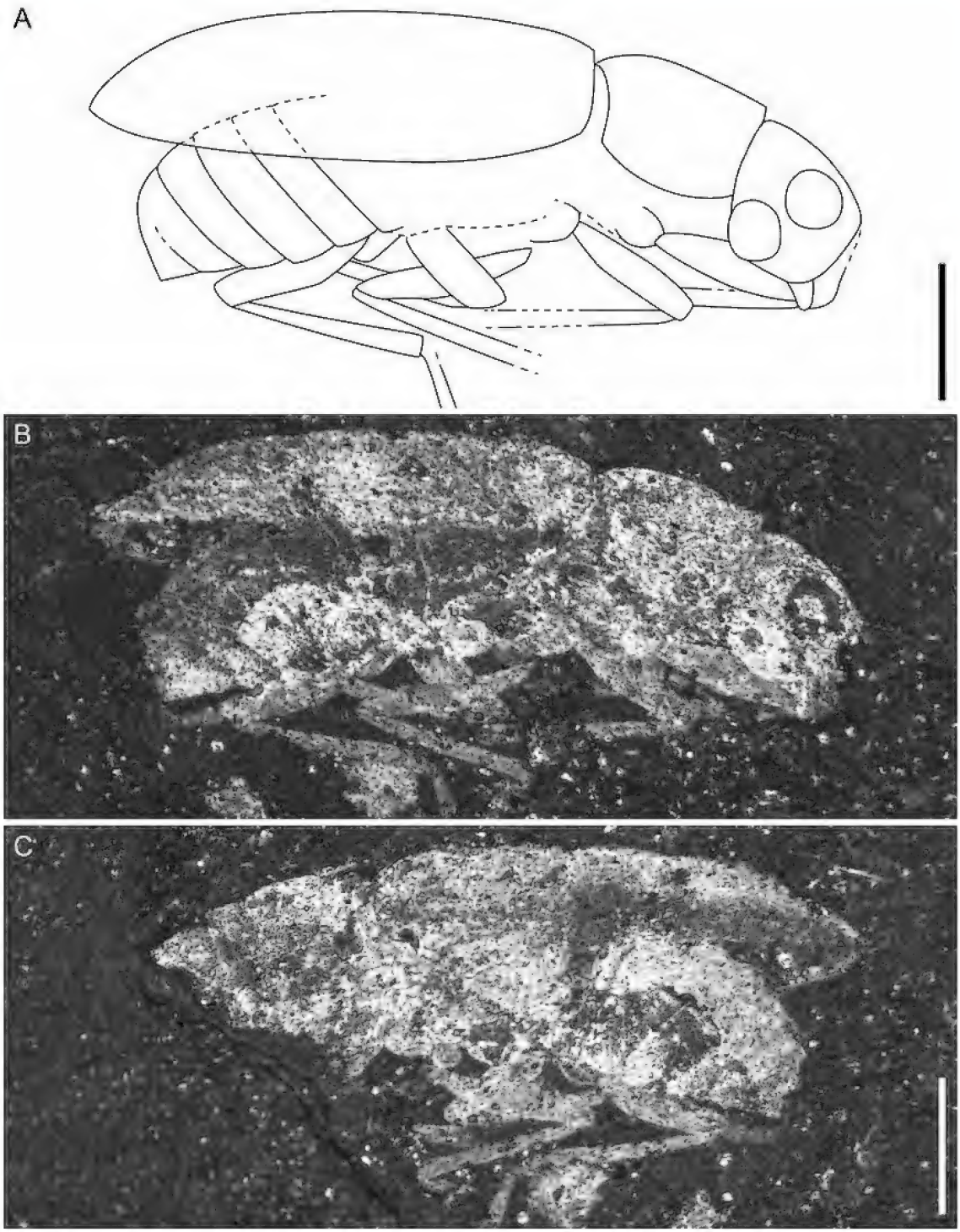

FIG. 25. Morphotype 22, VMNH 51822. **A, B.** Part. **C.** Counterpart. Scale bars: 1 mm.

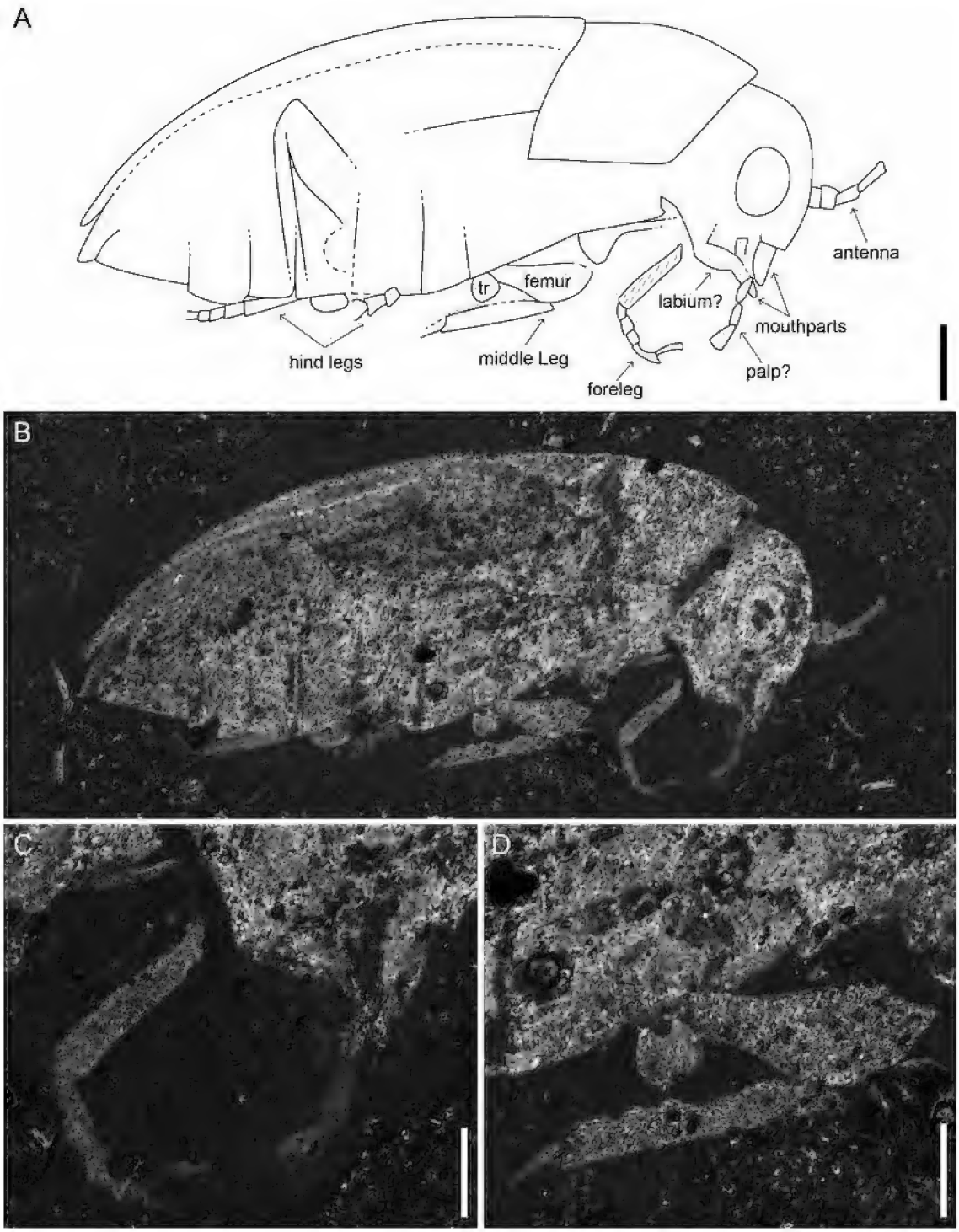

FIG. 26. Morphotype 23, VMNH 97984. **A, B.** Habitus. **C.** Mouthparts and foreleg. **D.** Middle leg. **tr** = trochanter. Scale bars: A, B: 0.5 mm; C, D: 0.25 mm.

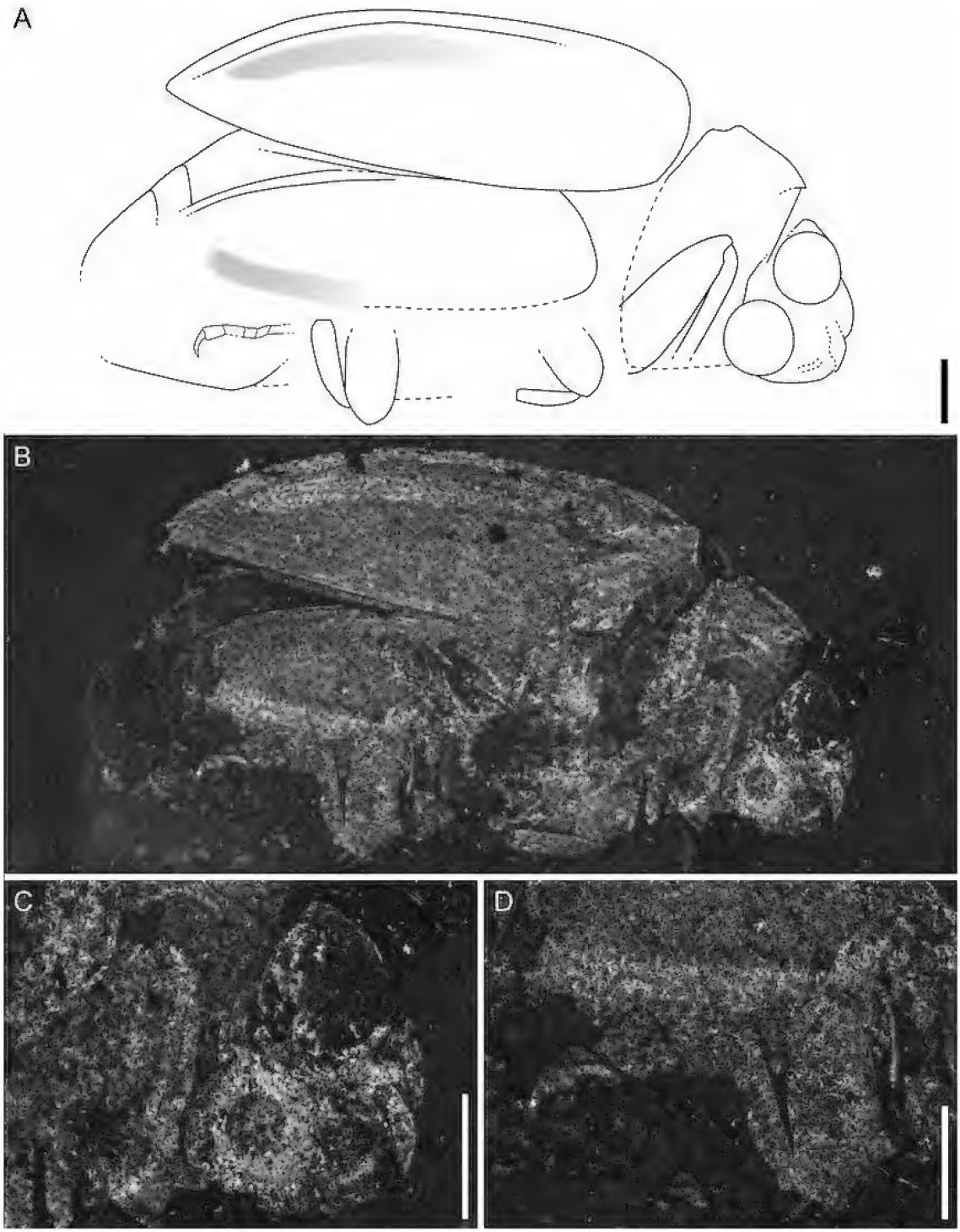

FIG. 27. Morphotype 24, VMNH 49593. **A, B.** Habitus. **C.** Head. **D.** Hind leg. Scale bars: 1 mm.

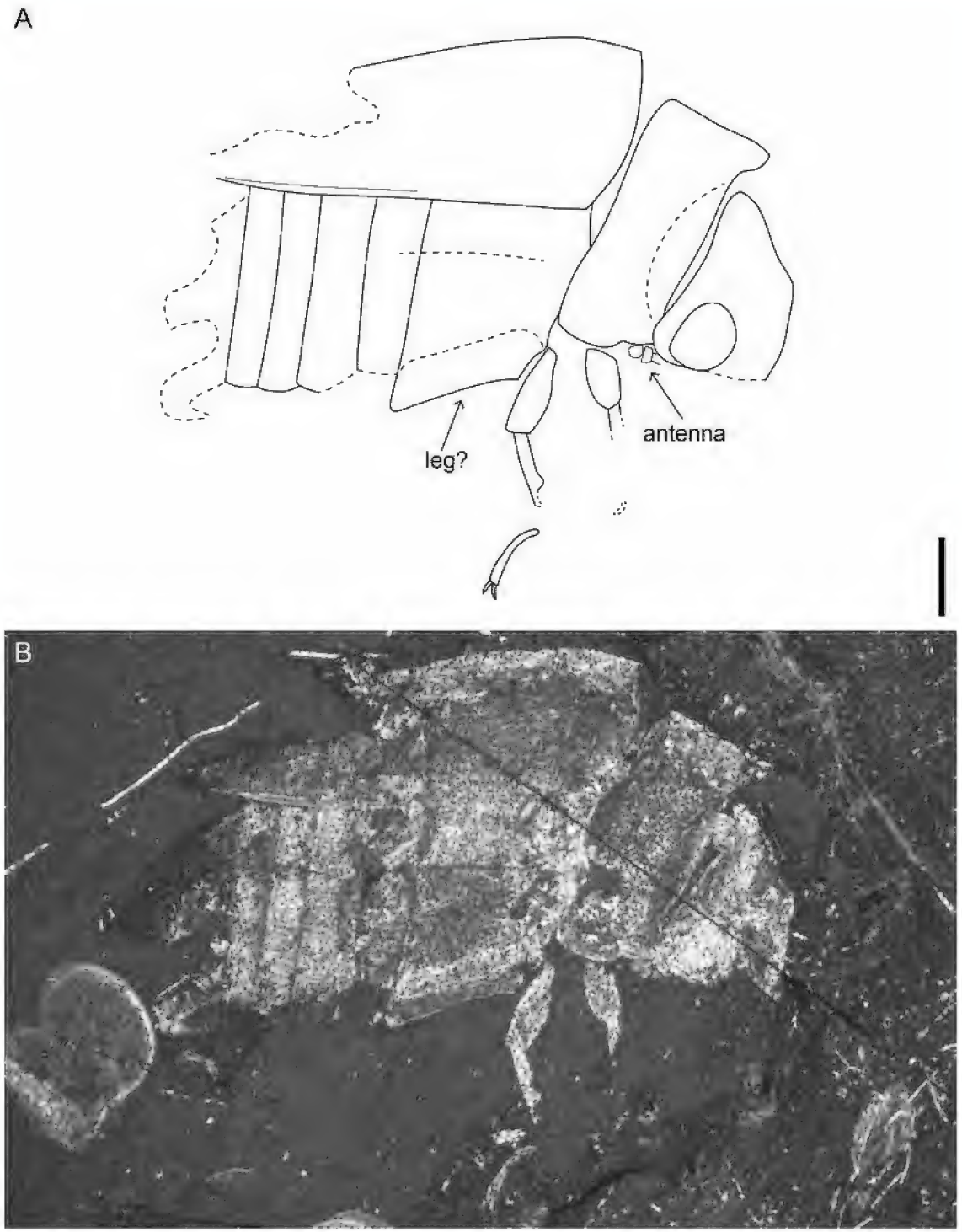

FIG. 28. Morphotype 25, AMNH 04-81. Scale bar: 1 mm.

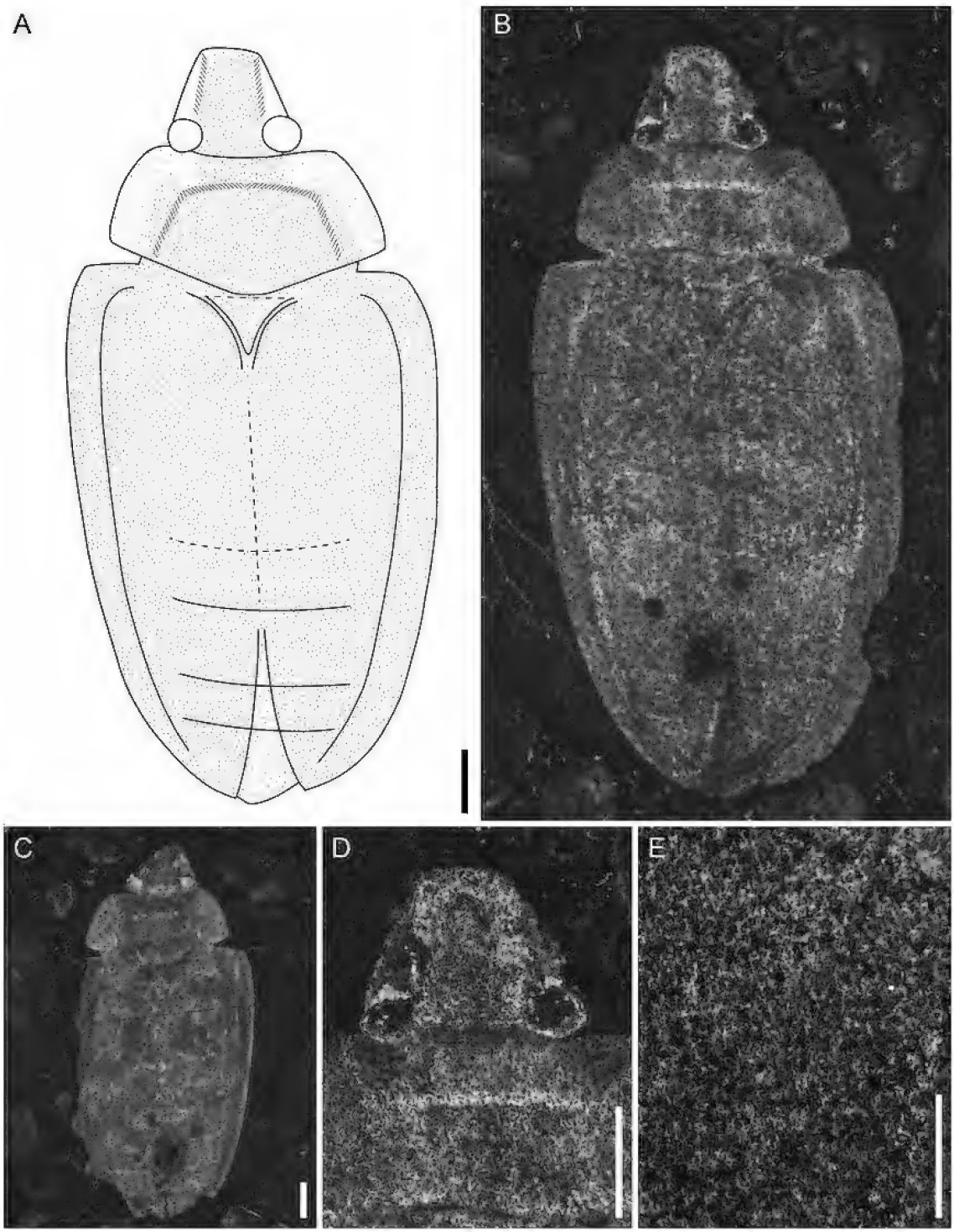

FIG. 29. Morphotype 26, VMNH 49650. **A, B.** Part. **C.** Counterpart. **D.** Head of part. **E.** Dense microtrichia covering elytra. Scale bars: A–D: 1 mm; E: 0.5 mm.

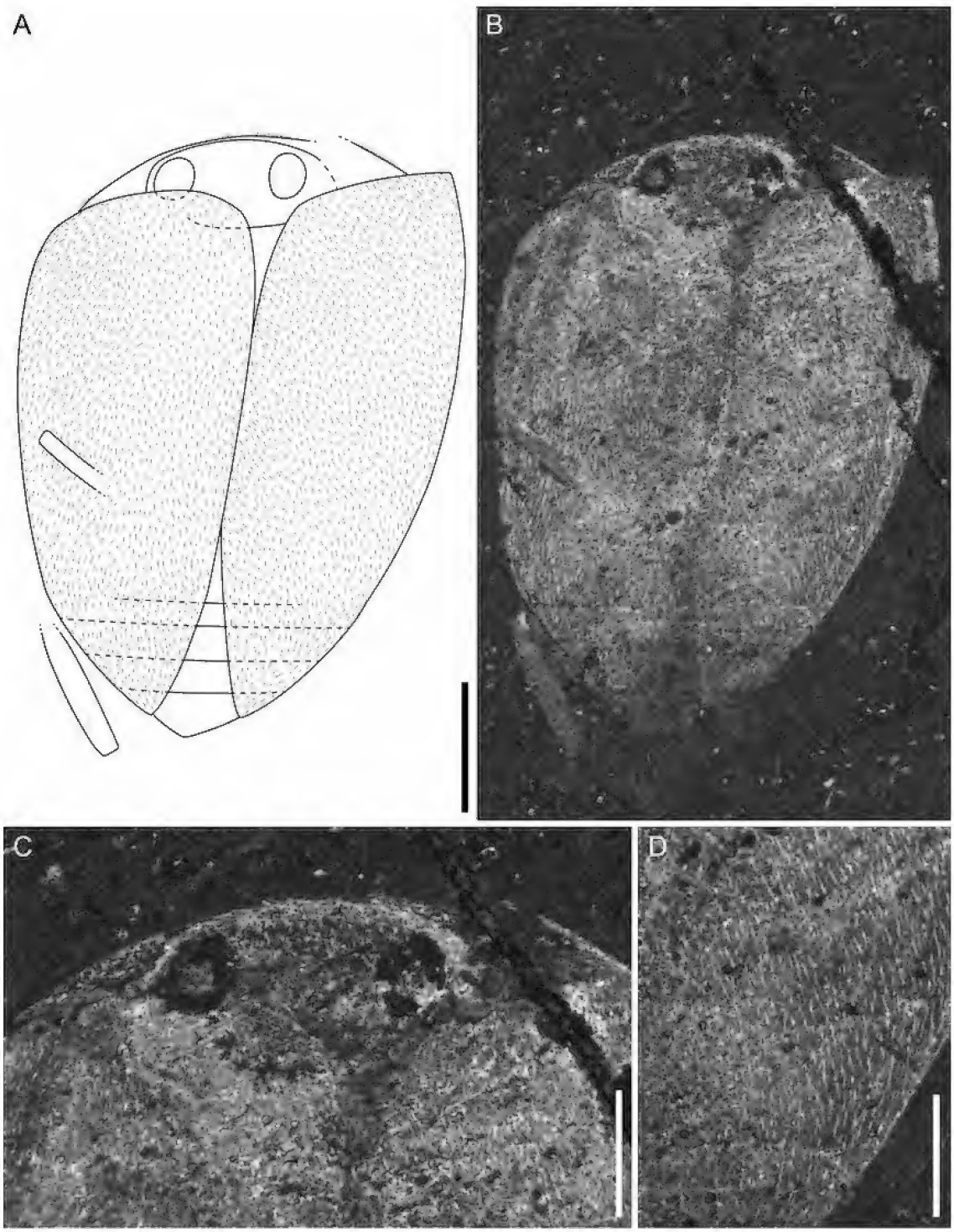

FIG. 30. Morphotype 27, VMNH 98157. **A, B.** Habitus. **C.** Head and anterior margins of elytra. **D.** Right elytron showing dense setae. Scale bars: A, B: 1 mm; C, D: 0.5 mm.

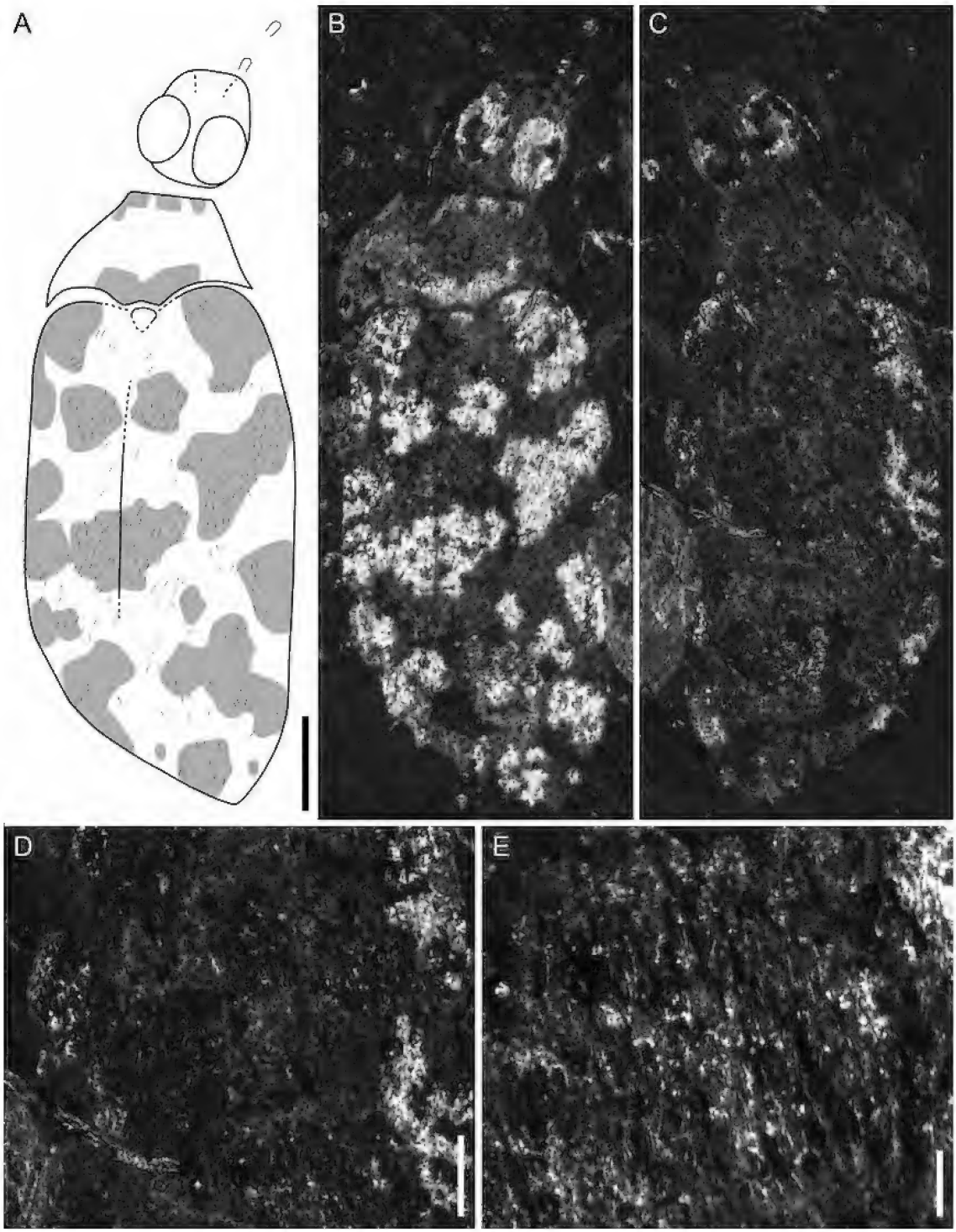

FIG. 31. Morphotype 28, AMNH 04-57. **A, B.** Part. **C.** Counterpart. **D, E.** Long setae on elytra of counterpart. Scale bars: A–C: 0.5 mm; D: 0.25 mm; E: 0.1 mm.

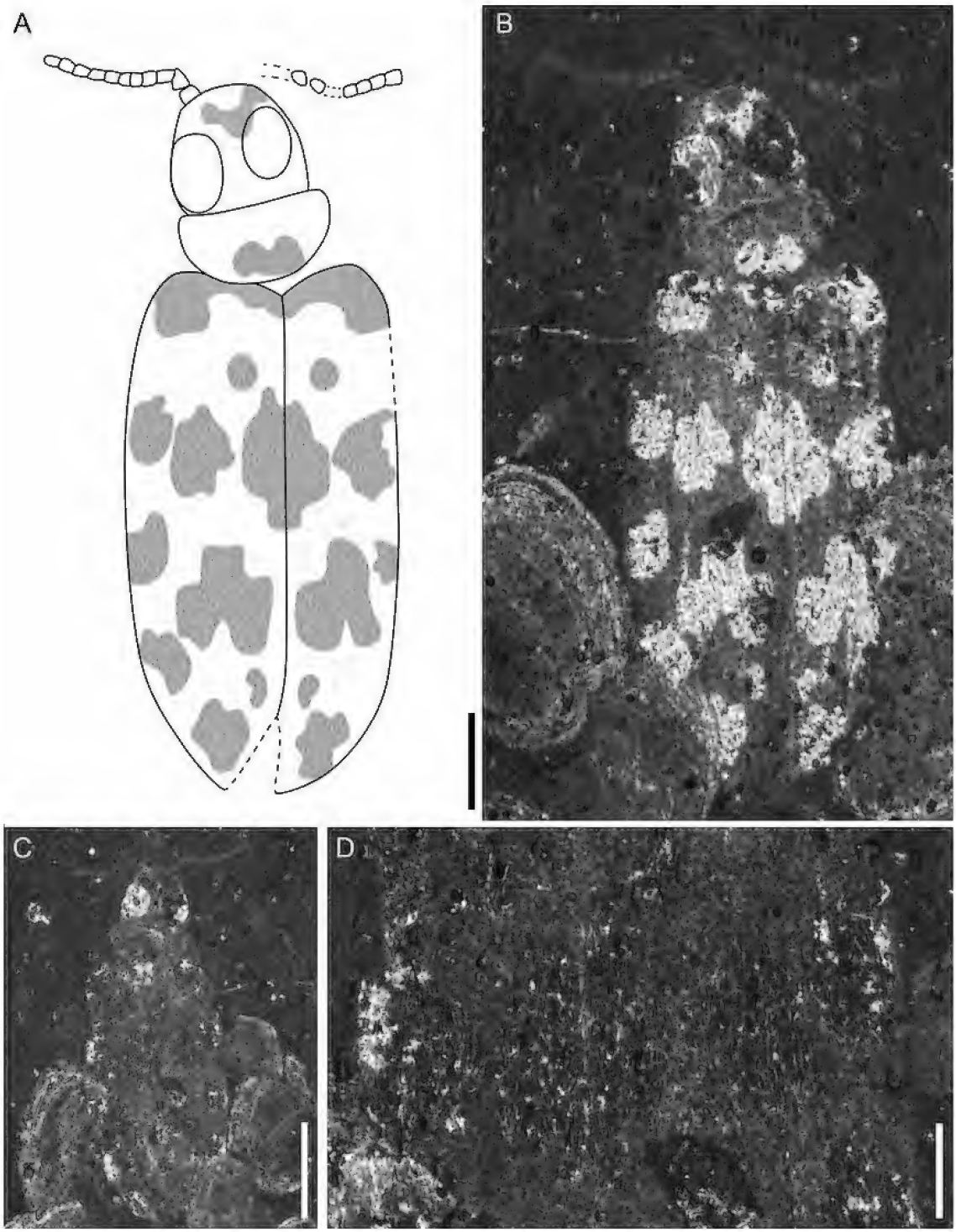

FIG. 32. Morphotype 29, VMNH 94607. **A, B.** Part. **C.** Counterpart. **D.** Long setae on elytra of counterpart. Scale bars: A, B: 0.5 mm; C: 1 mm; D: 0.25 mm.

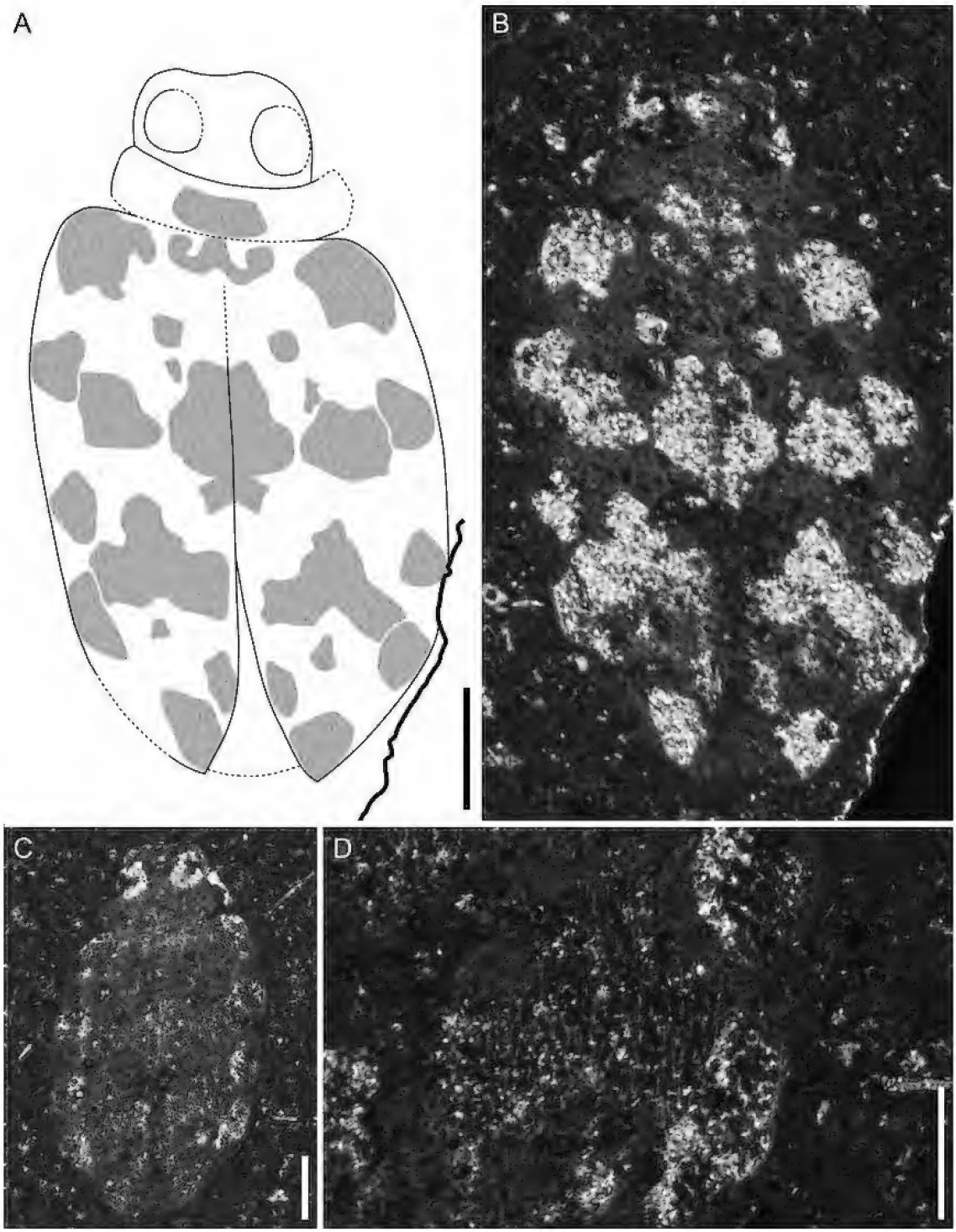

FIG. 33. Morphotype 30, AMNH 04-70. **A, B.** Part. **C.** Counterpart. **D.** Long setae on elytra of counterpart. Scale bars: A–C: 0.5 mm; D: 0.25 mm.

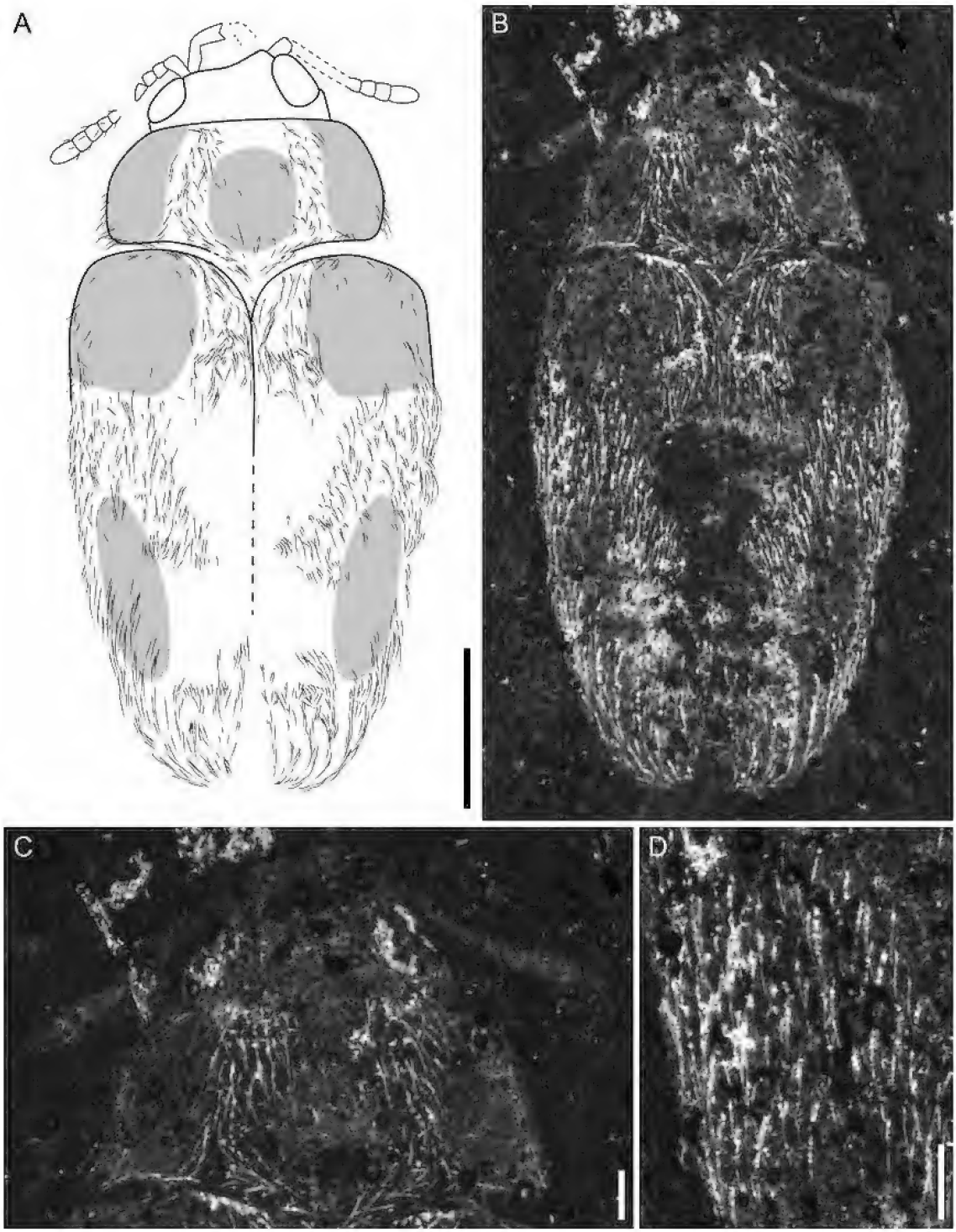

FIG. 34. Morphotype 31, VMNH 49764. **A, B.** Habitus. **C.** Head with antennae and partial mouthparts; pronotum showing distinct pattern of setae. **D.** Long, dense setae on left elytron. Scale bars: A, B: 0.5 mm; C, D: 0.1 mm.

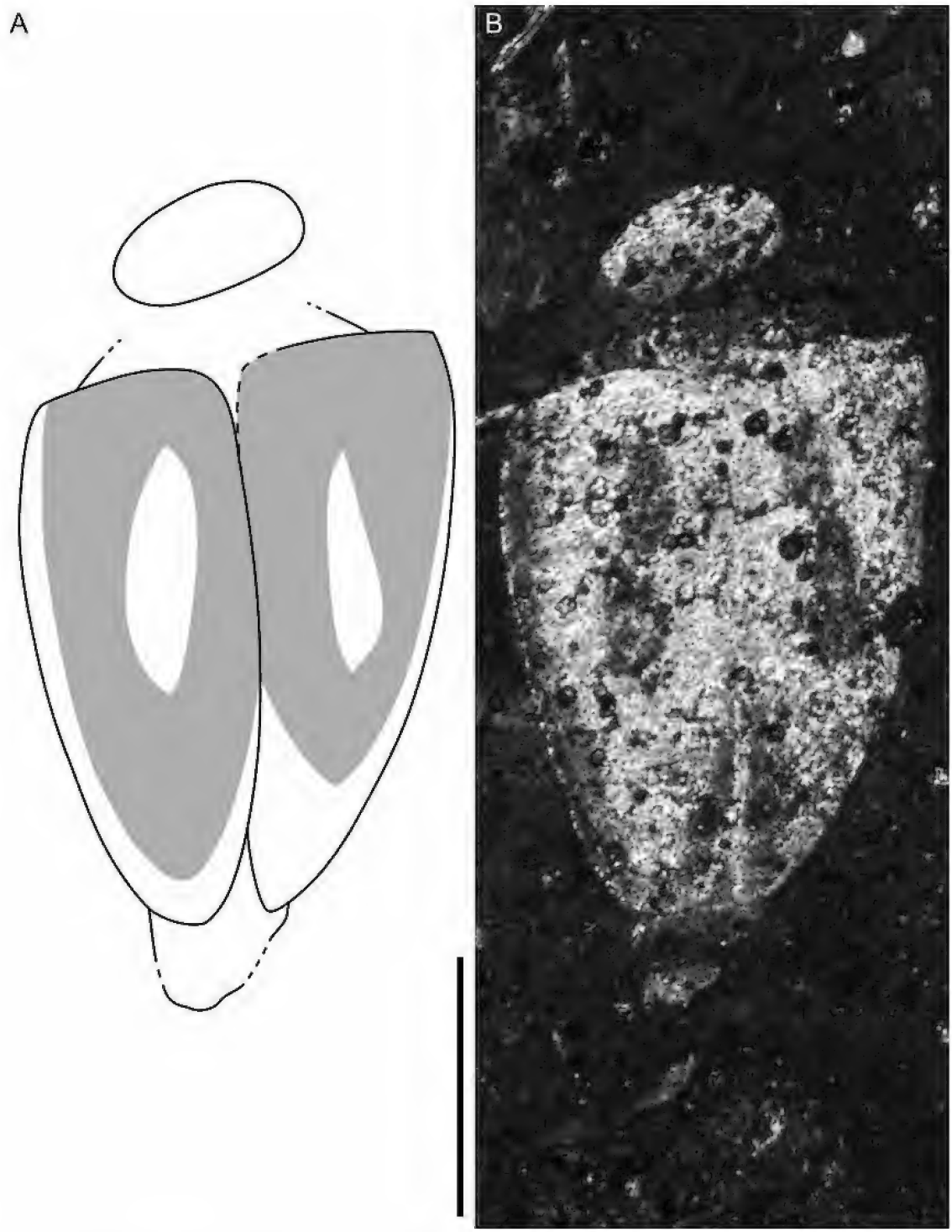

FIG. 35. Morphotype 32, VMNH 94723. Scale bar: 0.5 mm.

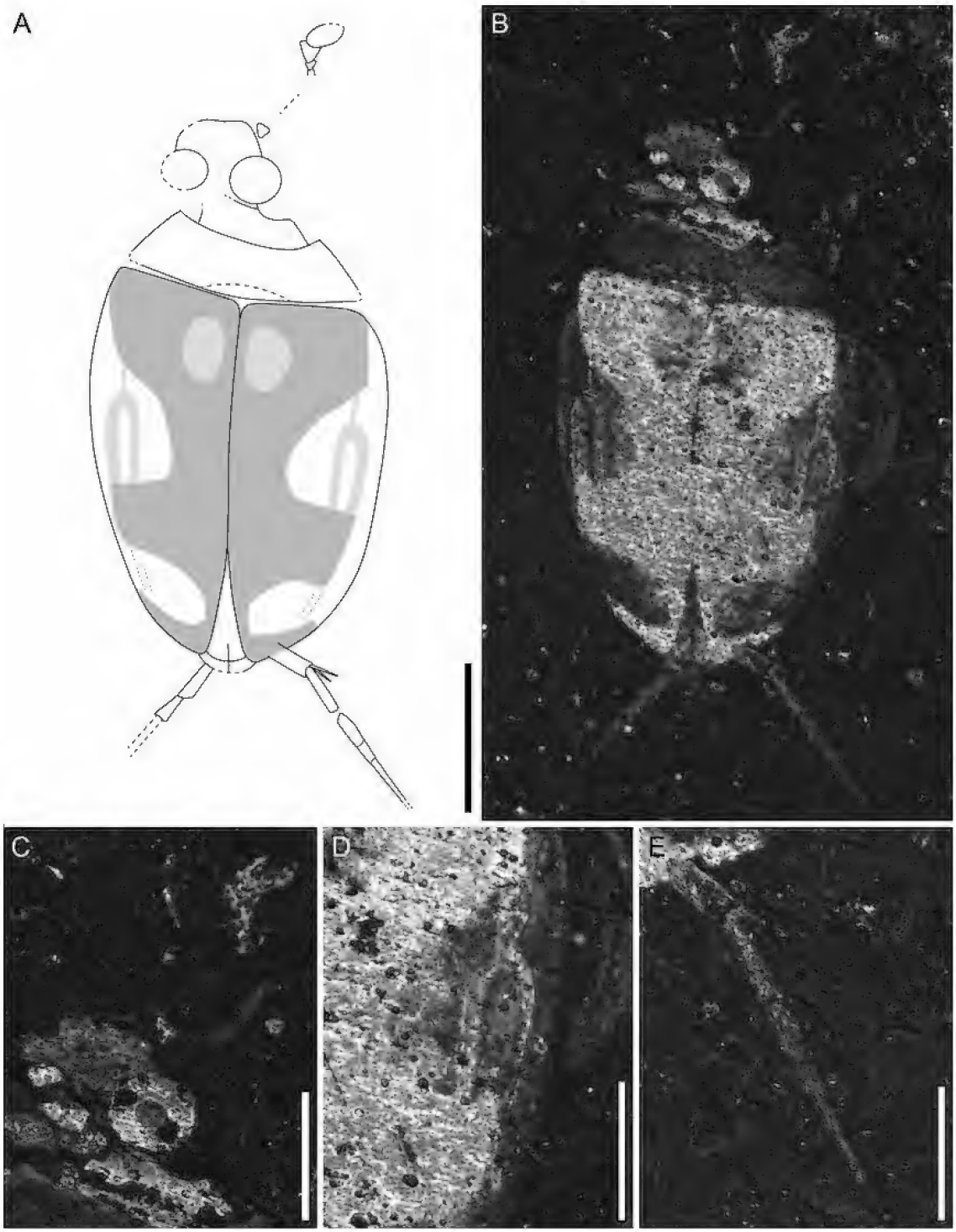

FIG. 36. Morphotype 33, YPM IP 035981. **A, B.** Habitus. **C.** Head with partial antenna. **D.** Right elytron showing forklike structure, possibly wing veins. **E.** Right hind leg showing distinct tibial spurs. Scale bars: A, B: 1 mm; C–E: 0.5 mm.

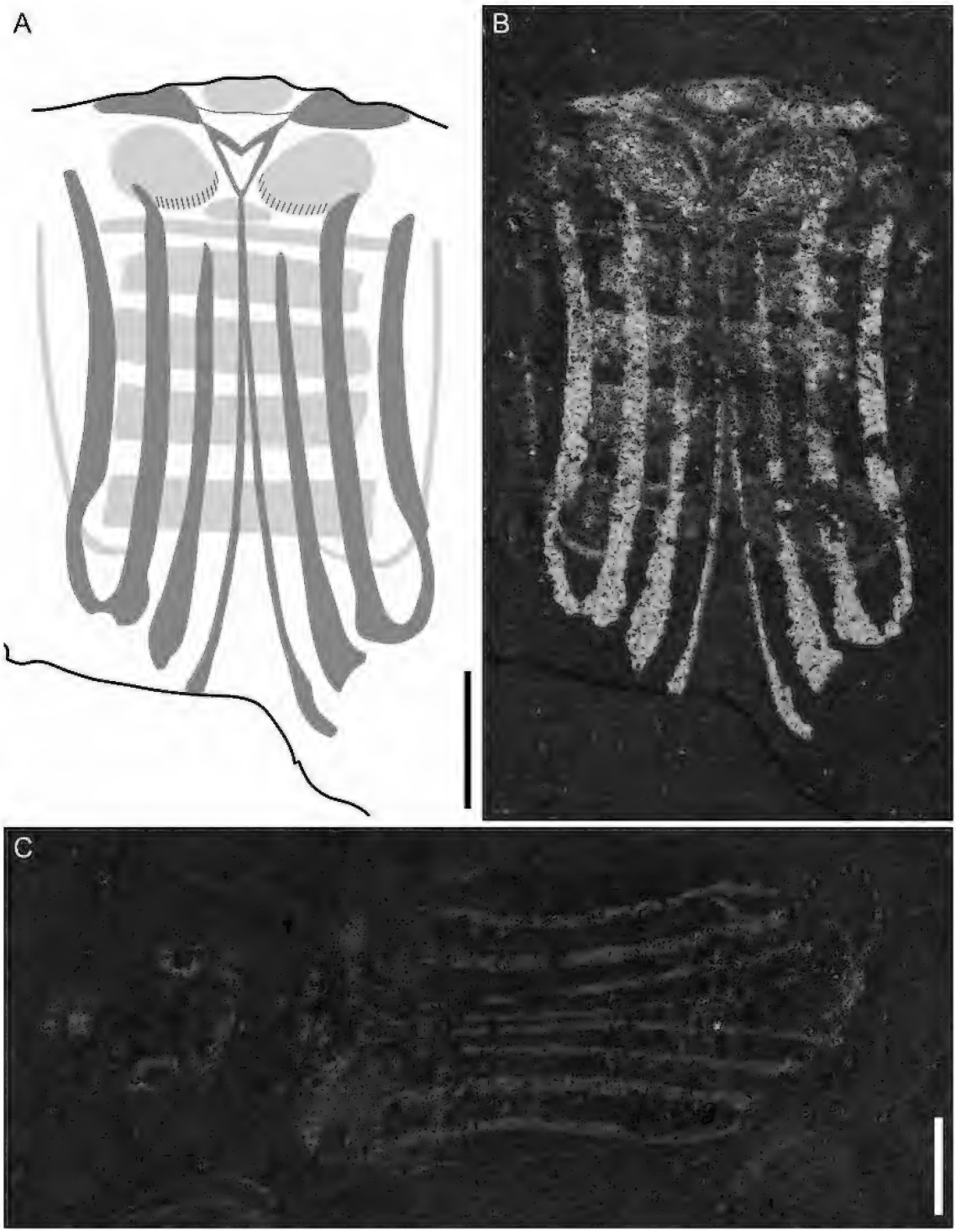

FIG. 37. *Holcoptera solitensis*. **A, B.** VMNH 97986. **C.** VMNH 96762 with partial head. Scale bars: 1 mm.

FIG. 38. *Holcoptera* sp., AMNH 04-96. Note width of second innermost longitudinal bands compared to those of VMNH 97986 and 96762 (fig. 37). Specimen possibly belonging to a separate holcopteran species. Scale bar: 1 mm.

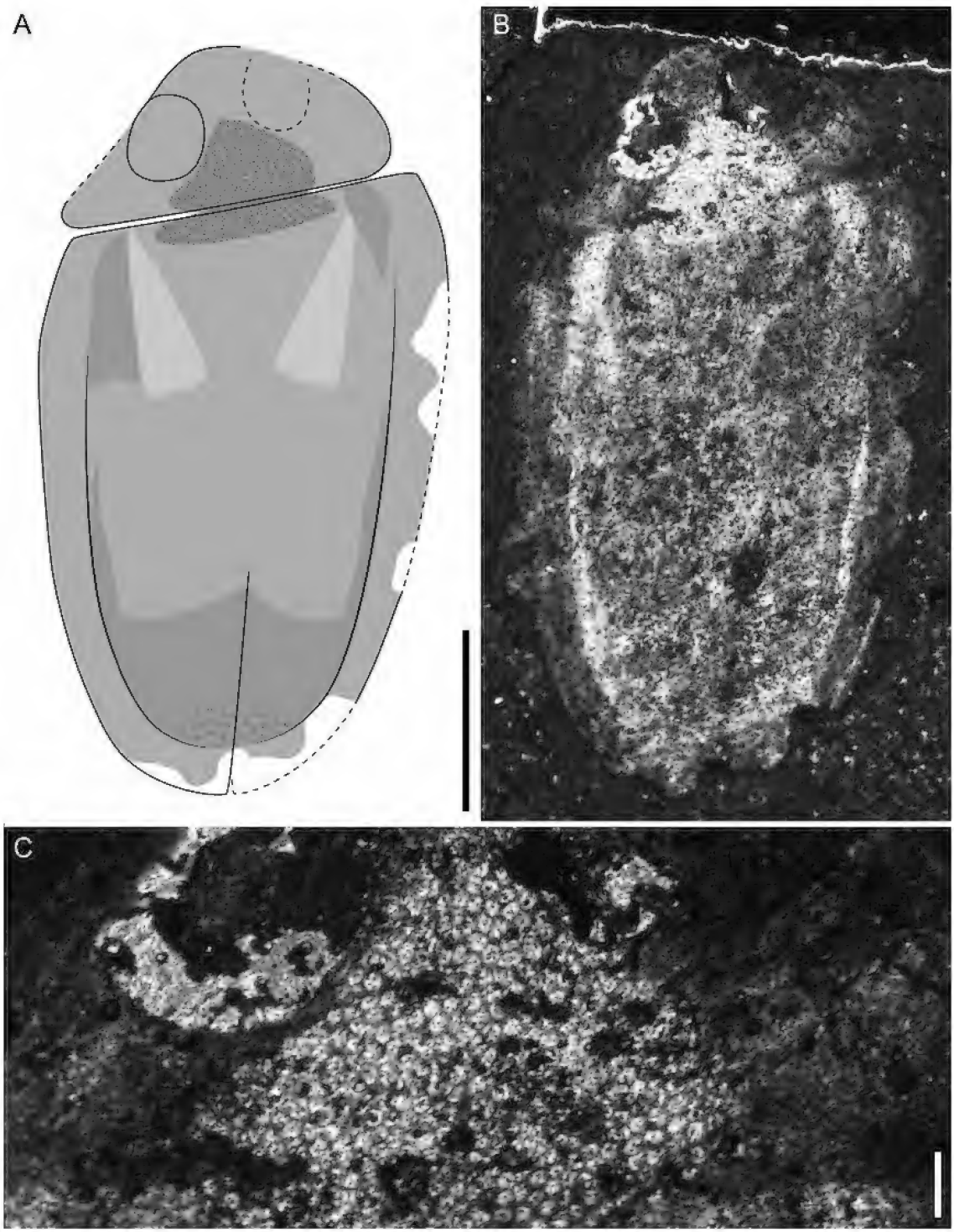

FIG. 39. Morphotype 34, AMNH 04-50. **A, B.** Habitus. **C.** Head showing distinct patch of nodules behind the eyes. Scale bars: A, B: 1 mm; C: 0.1 mm.

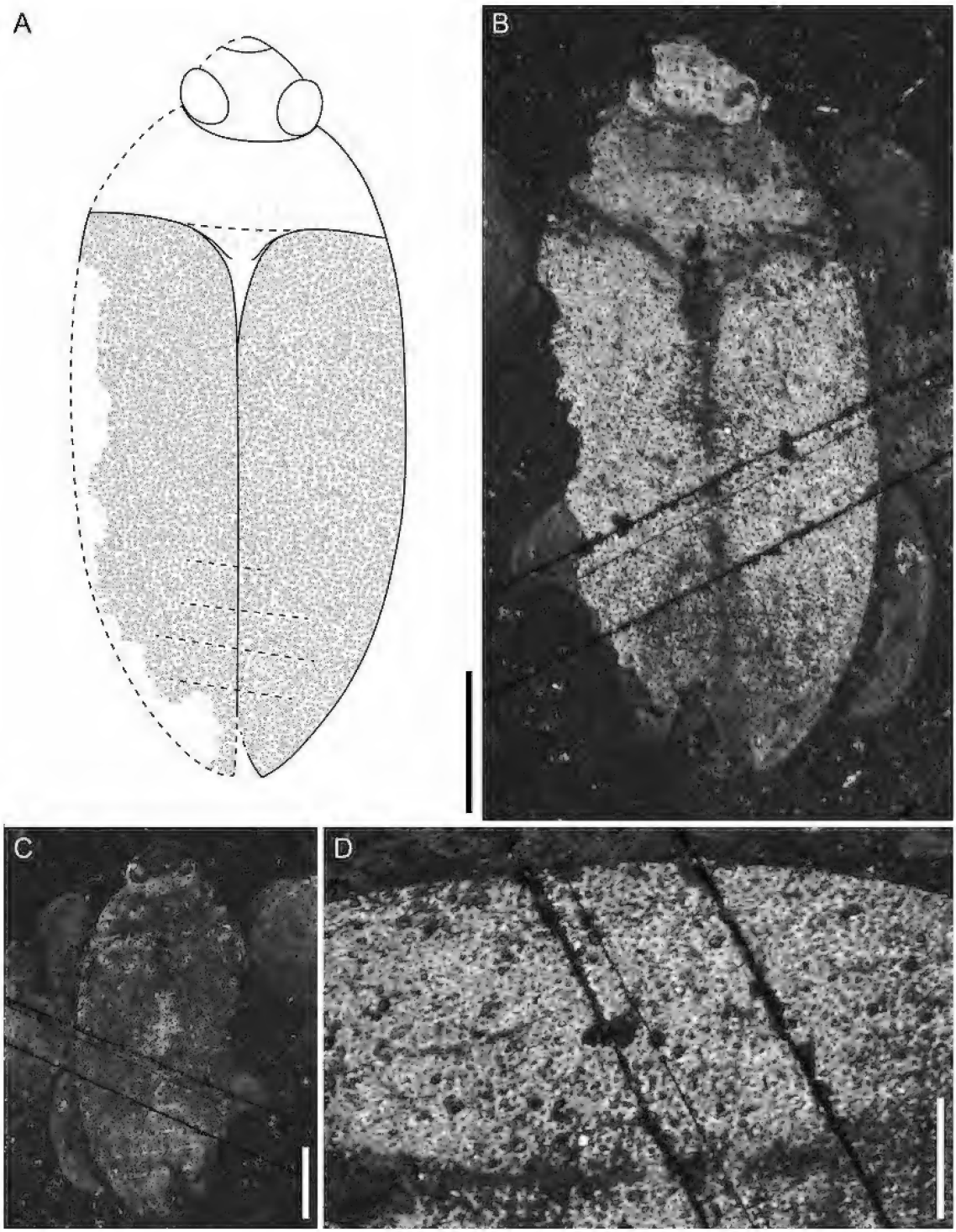

FIG. 40. Morphotype 35, VMNH 49742. **A, B.** Part. **C.** Counterpart. **D.** Right elytron of part covered in dense nodules. Scale bars: A–C: 1 mm; D: 0.5 mm.

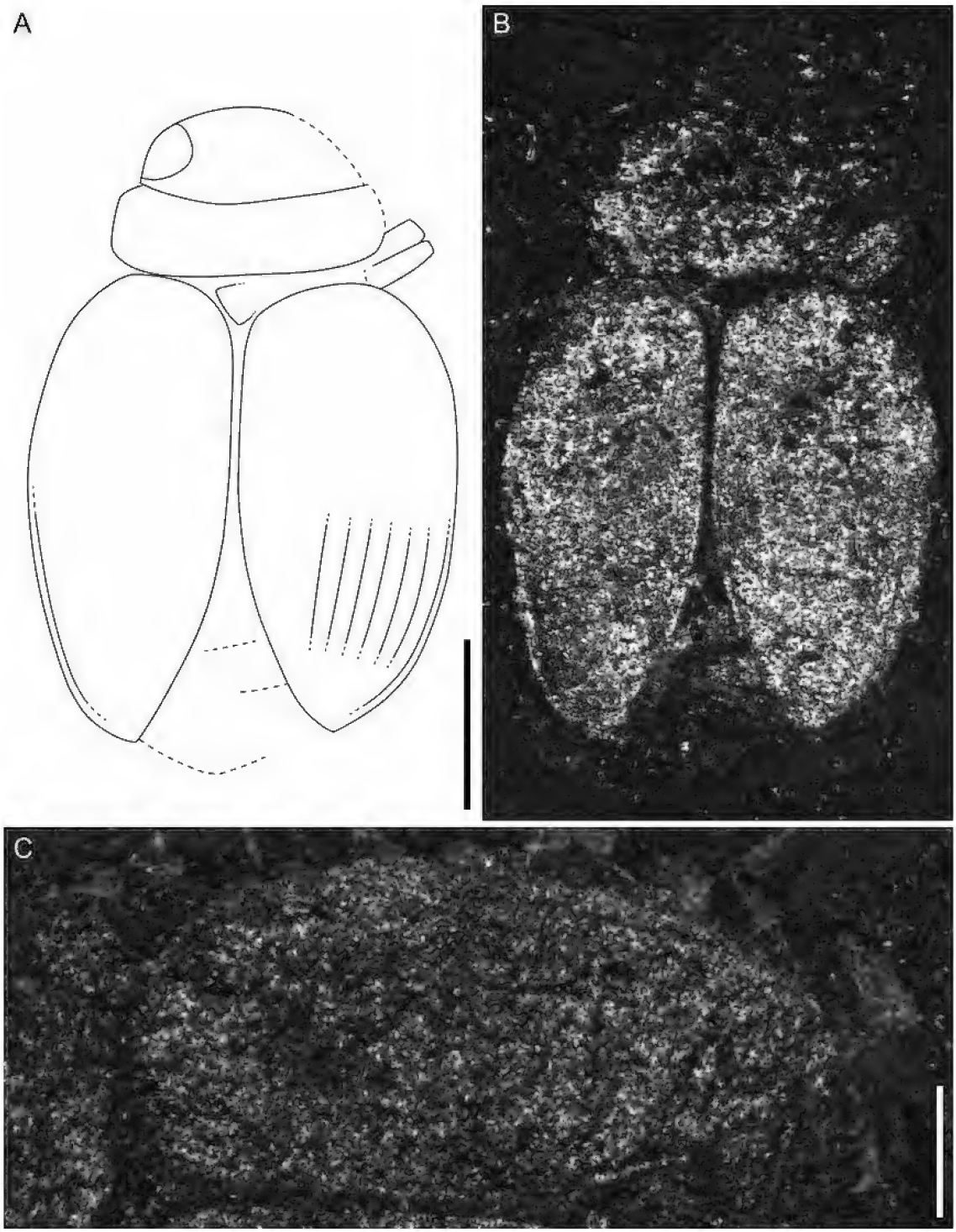

FIG. 41. Morphotype 36, AMNH 04-92. **A, B.** Habitus. **C.** Right elytron showing faint elytral striae. Photograph taken without ethanol and specimen tilted at an angle. Scale bars: A, B: 1 mm; C: 0.5 mm.

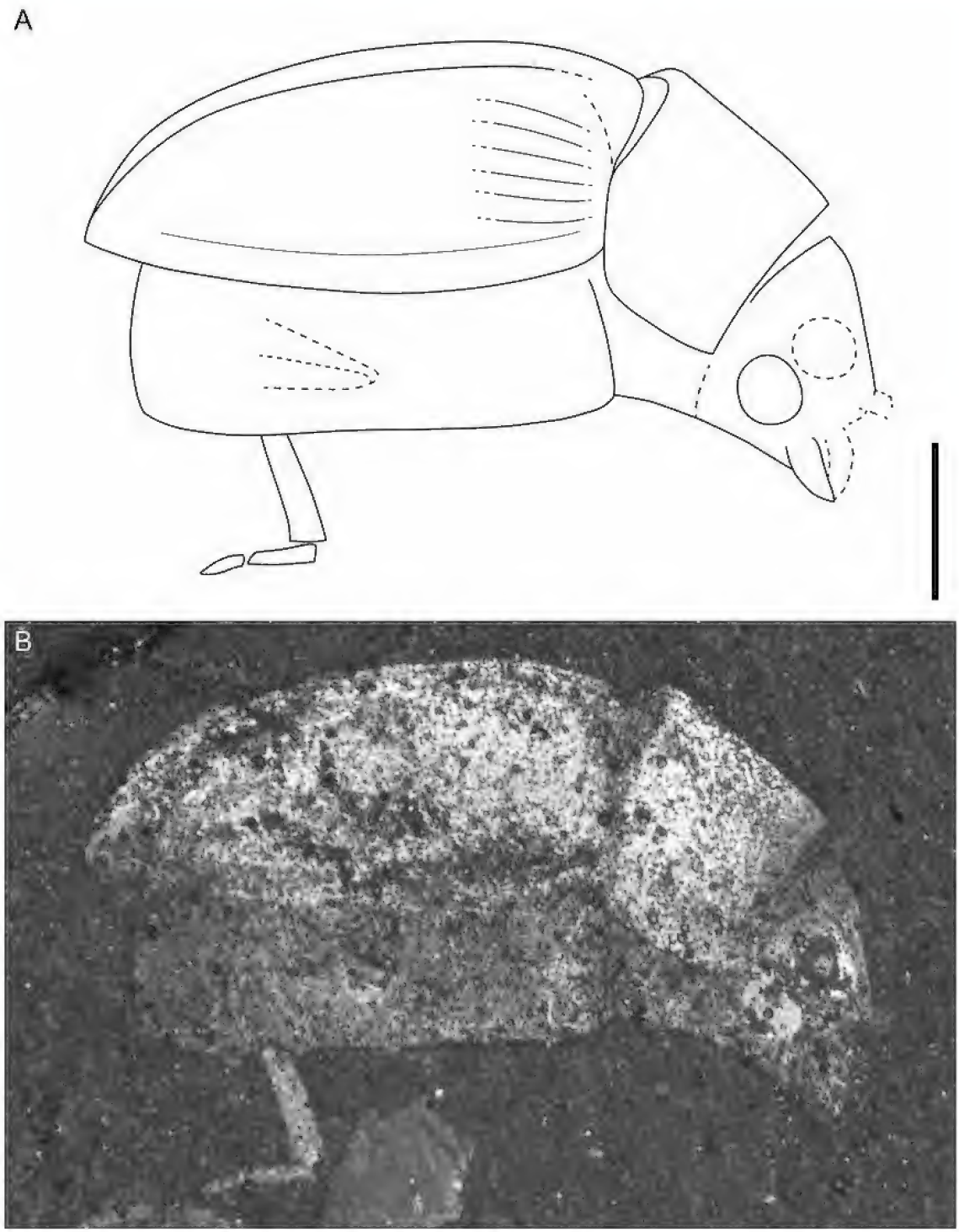

FIG. 42. Morphotype 37, VMNH 129484. Scale bar: 0.5 mm.

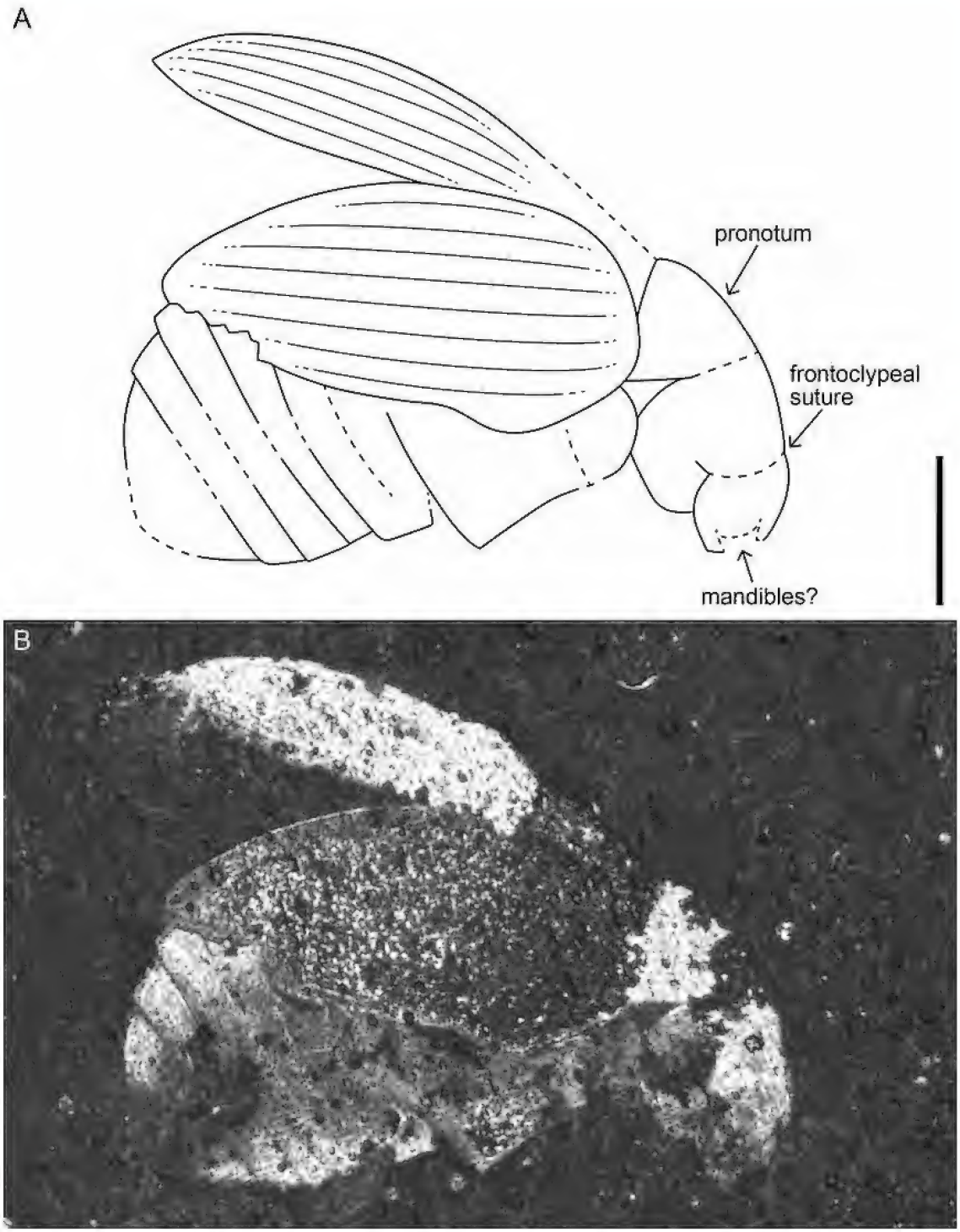

FIG. 43. Morphotype 38, VMNH 49659. Scale bar: 0.5 mm.

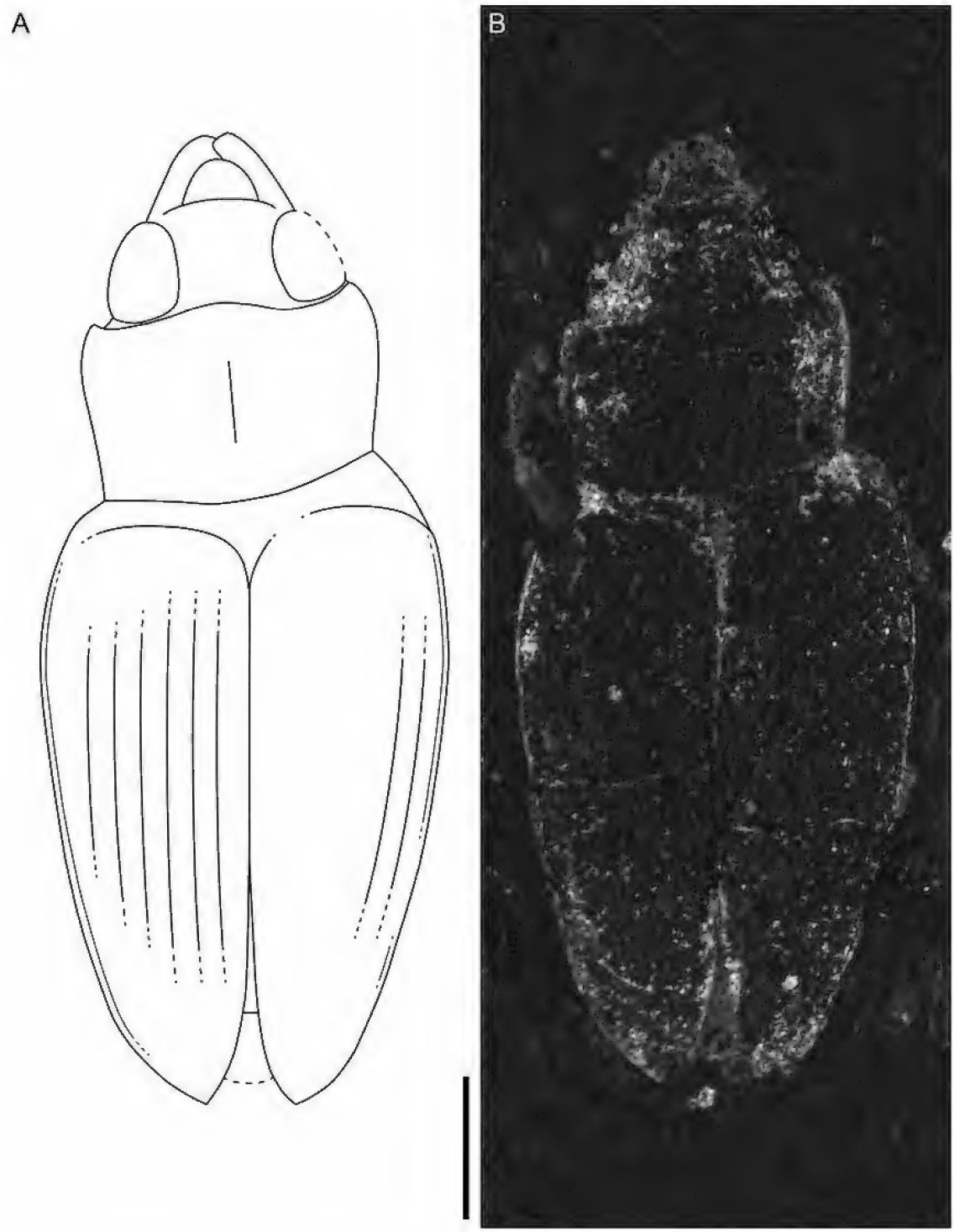

FIG. 44. Morphotype 39, VMNH 94814. Scale bar: 0.5 mm.

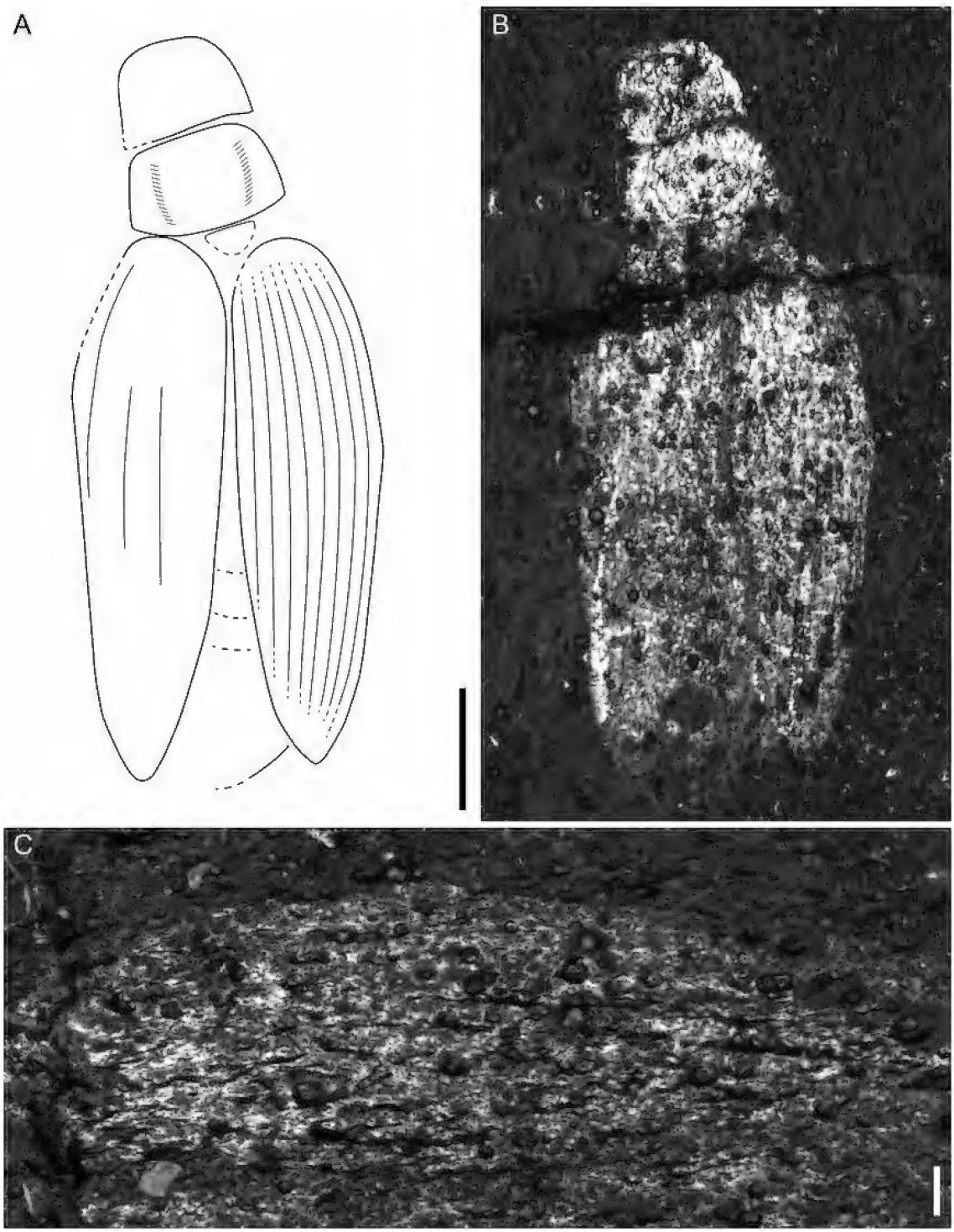

FIG. 45. Morphotype 40, AMNH 04-89. **A, B.** Habitus. **C.** Right elytron showing elytral striae. Photograph taken without ethanol and specimen tilted at an angle. Scale bars: A, B: 0.5 mm; C: 0.1 mm.

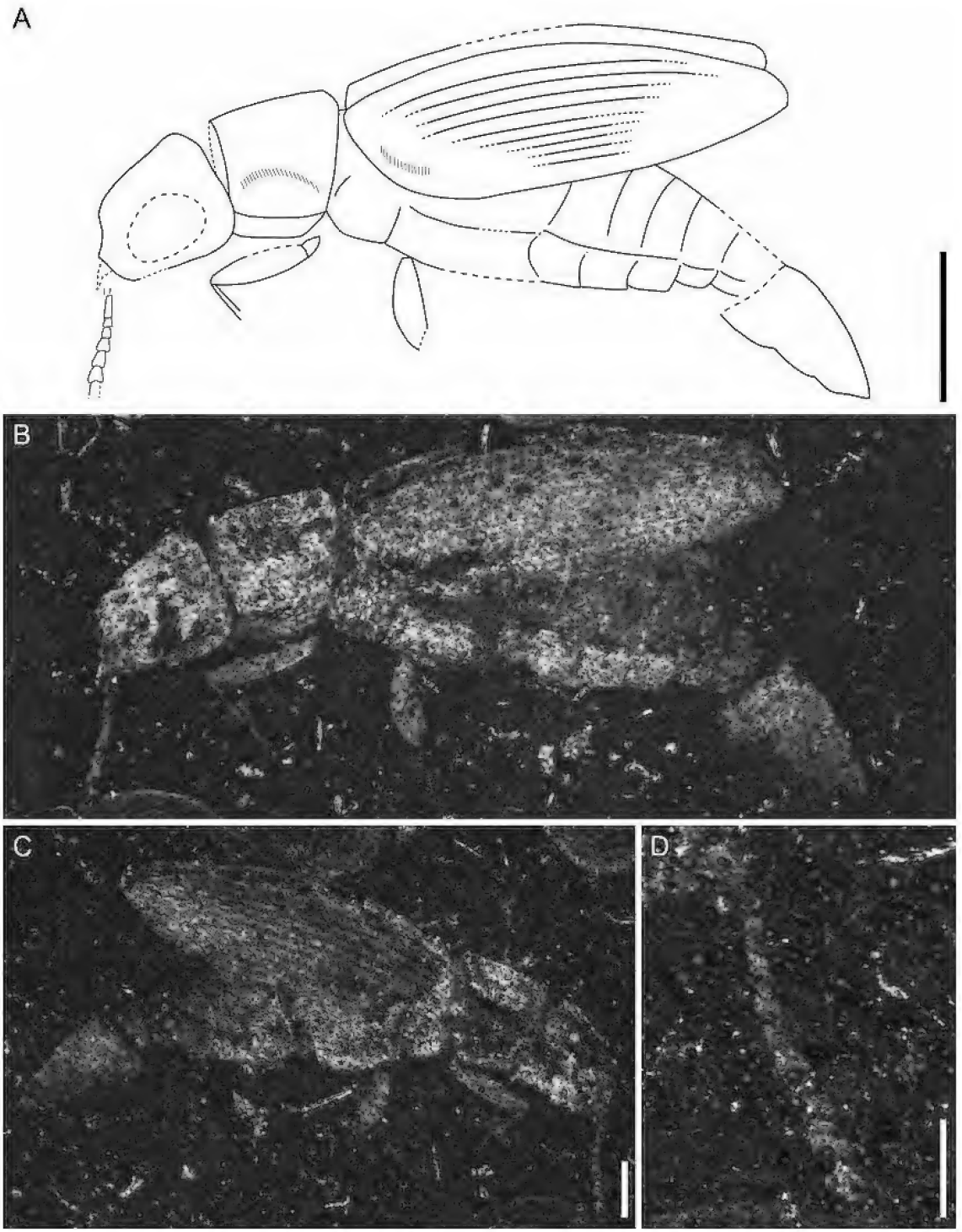

FIG. 46. Morphotype 41, YPM IP 036434. **A, B.** Part. **C.** Counterpart. **D.** Antenna of counterpart. Scale bars: A, B: 1 mm; C: 0.5 mm; D: 0.25 mm.

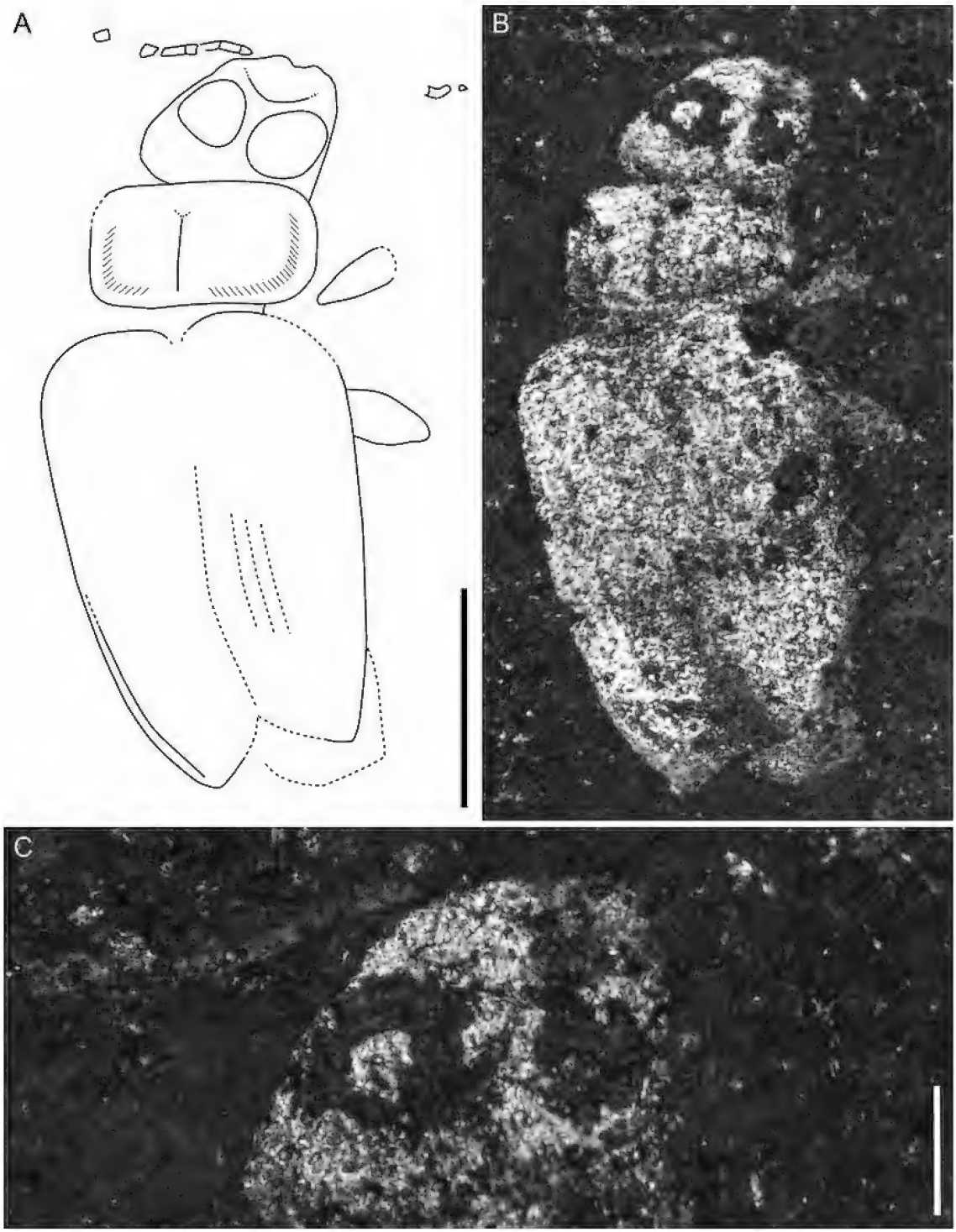

FIG. 47. Morphotype 42, VMNH 50226. **A, B.** Habitus. **C.** Head and partial left antenna. Scale bars: A, B: 1 mm; C: 0.25 mm.

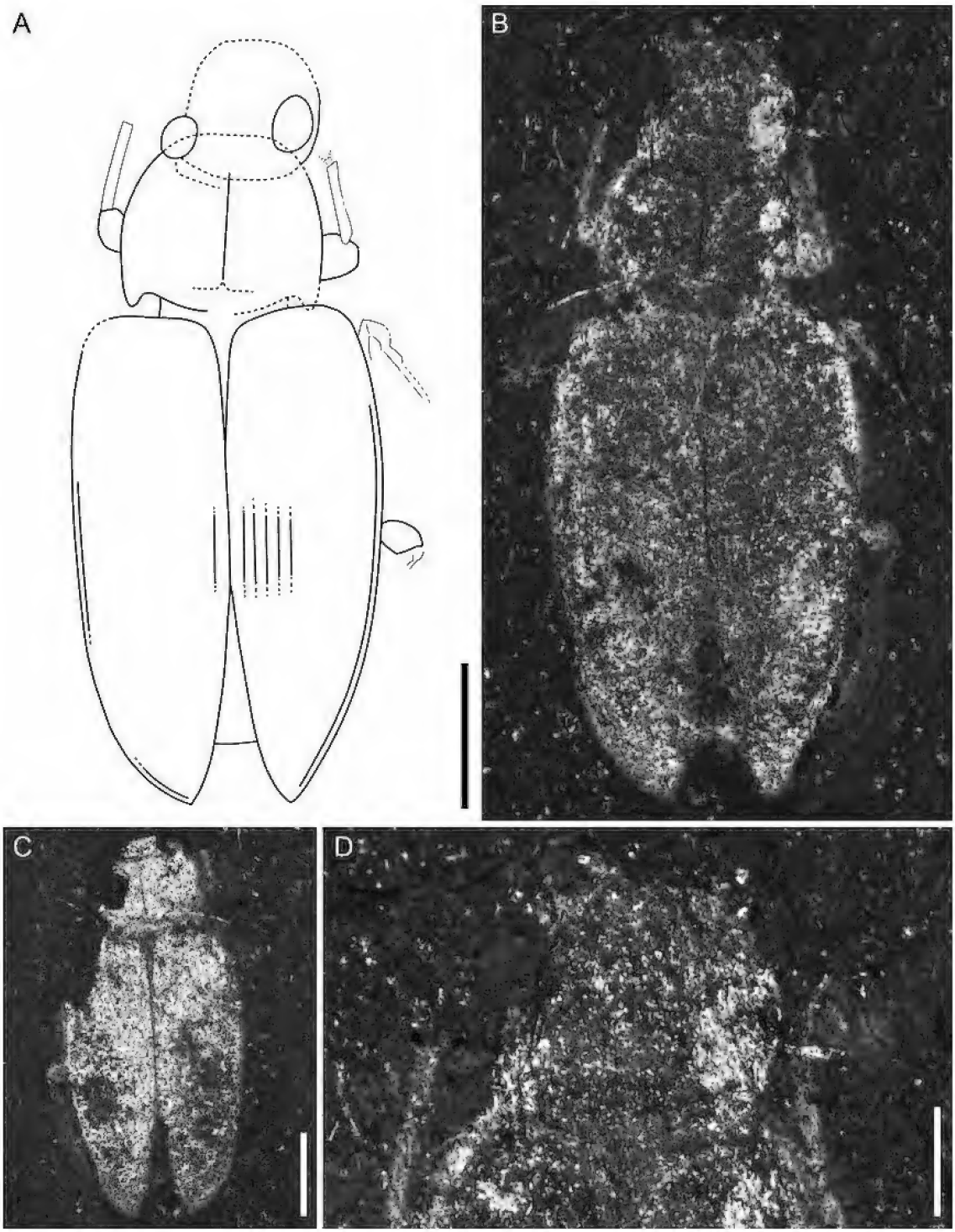

FIG. 48. Morphotype 43, VMNH 50190. **A, B.** Part. **C.** Counterpart, head not preserved. **D.** Head of part. Scale bars: A–C: 1 mm; D: 0.5 mm.

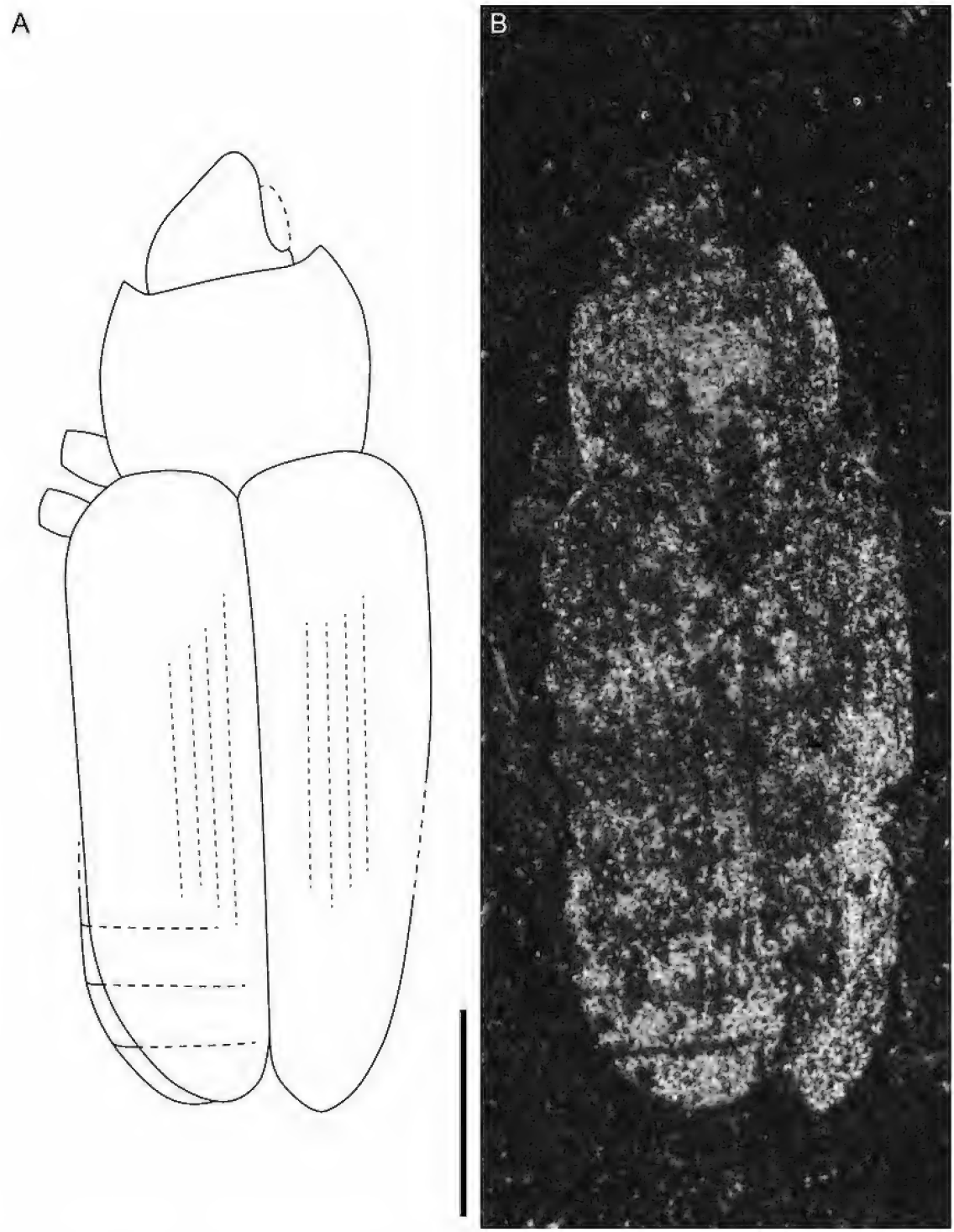

FIG. 49. Morphotype 44, VMNH 93596. Scale bar: 1 mm.

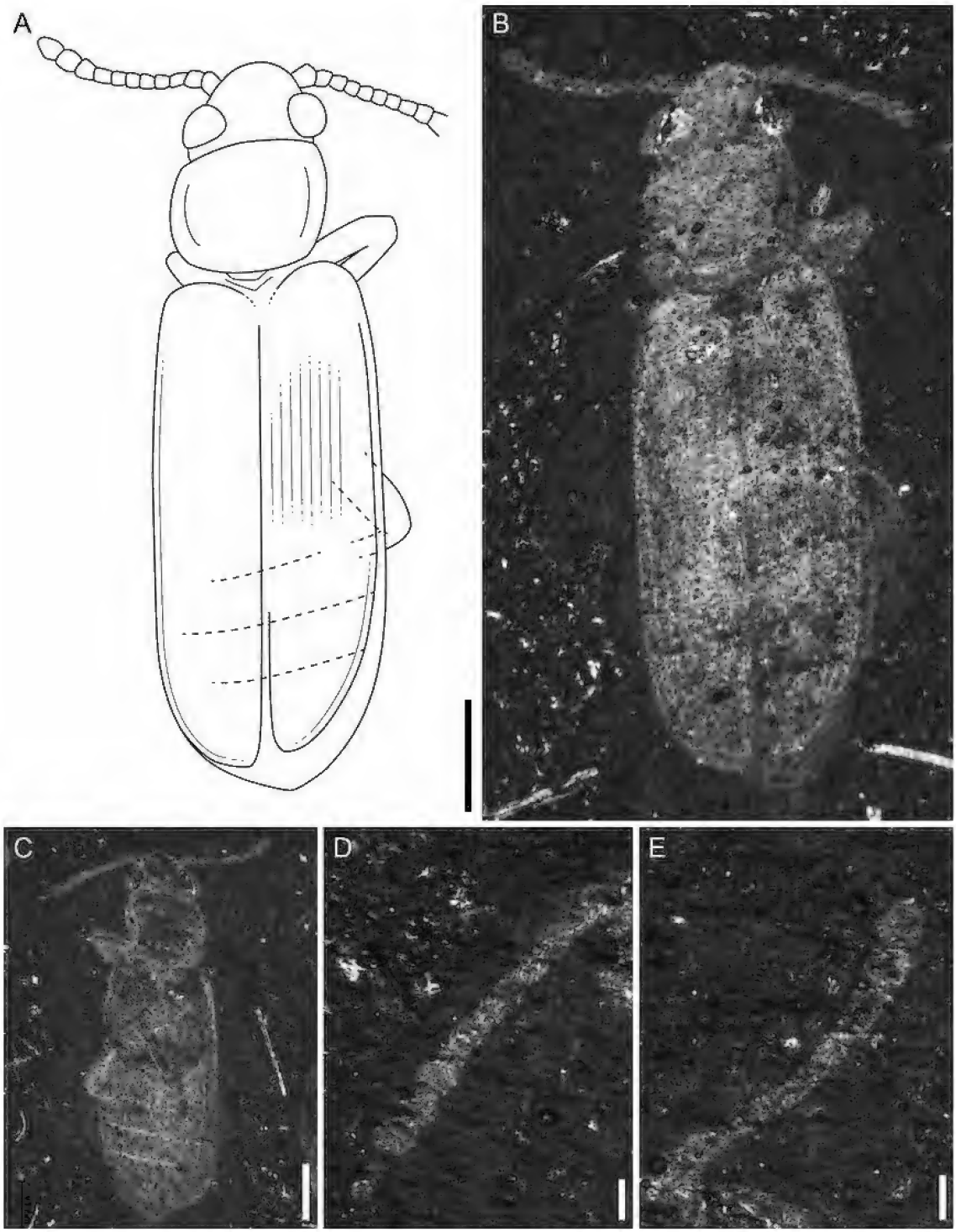

FIG. 50. Morphotype 45, VMNH 91682. **A, B.** Part. **C.** Counterpart. **D.** Left antenna of counterpart. **E.** Right antenna of counterpart. Scale bars: A–C: 0.5 mm; D, E: 0.1 mm.

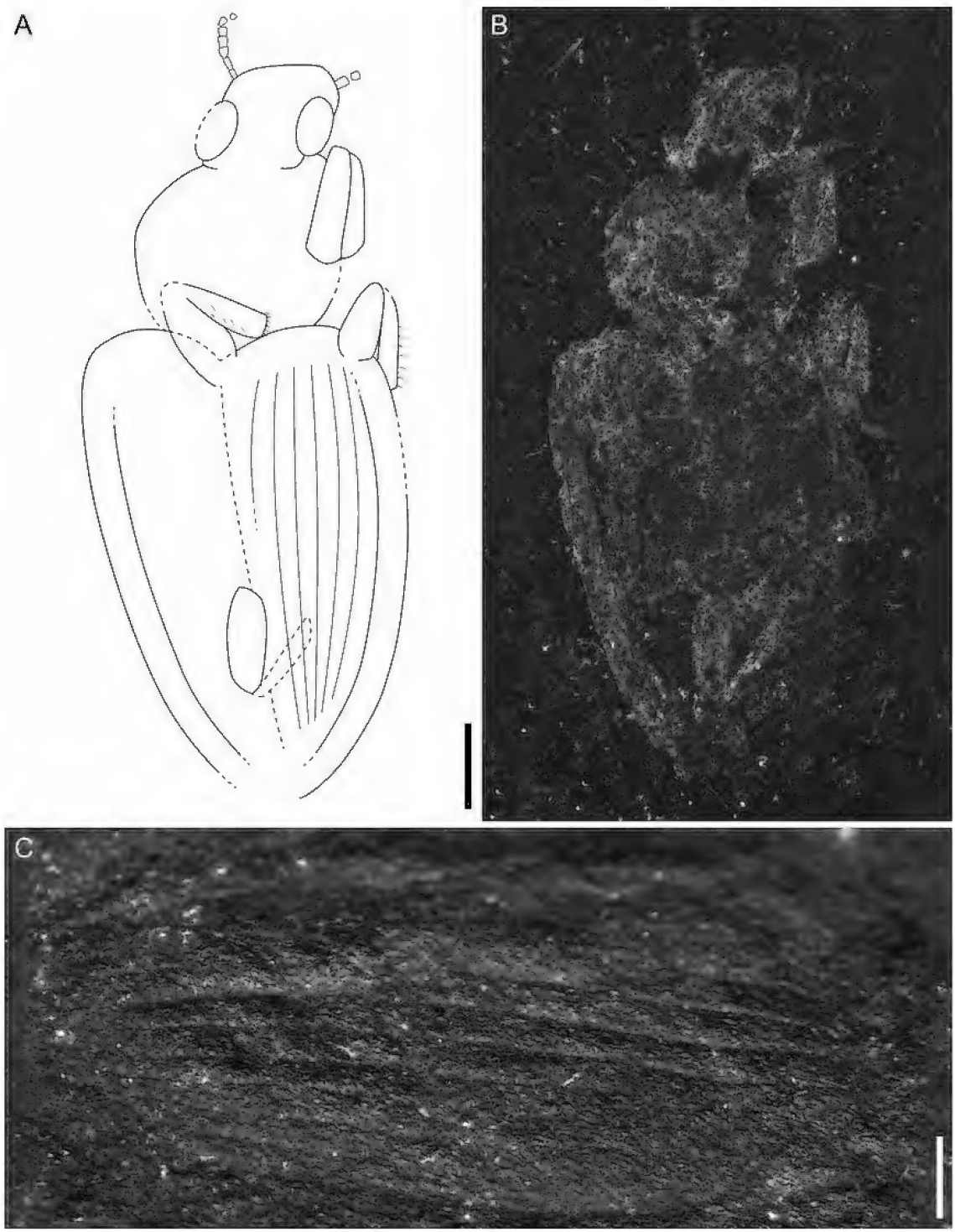

FIG. 51. Morphotype 46, YPM IP 388741. **A, B.** Habitus. **C.** Right elytron showing elytral striae. Photograph taken without ethanol and specimen tilted at an angle. Scale bars: A, B: 1 mm; C: 0.5 mm.

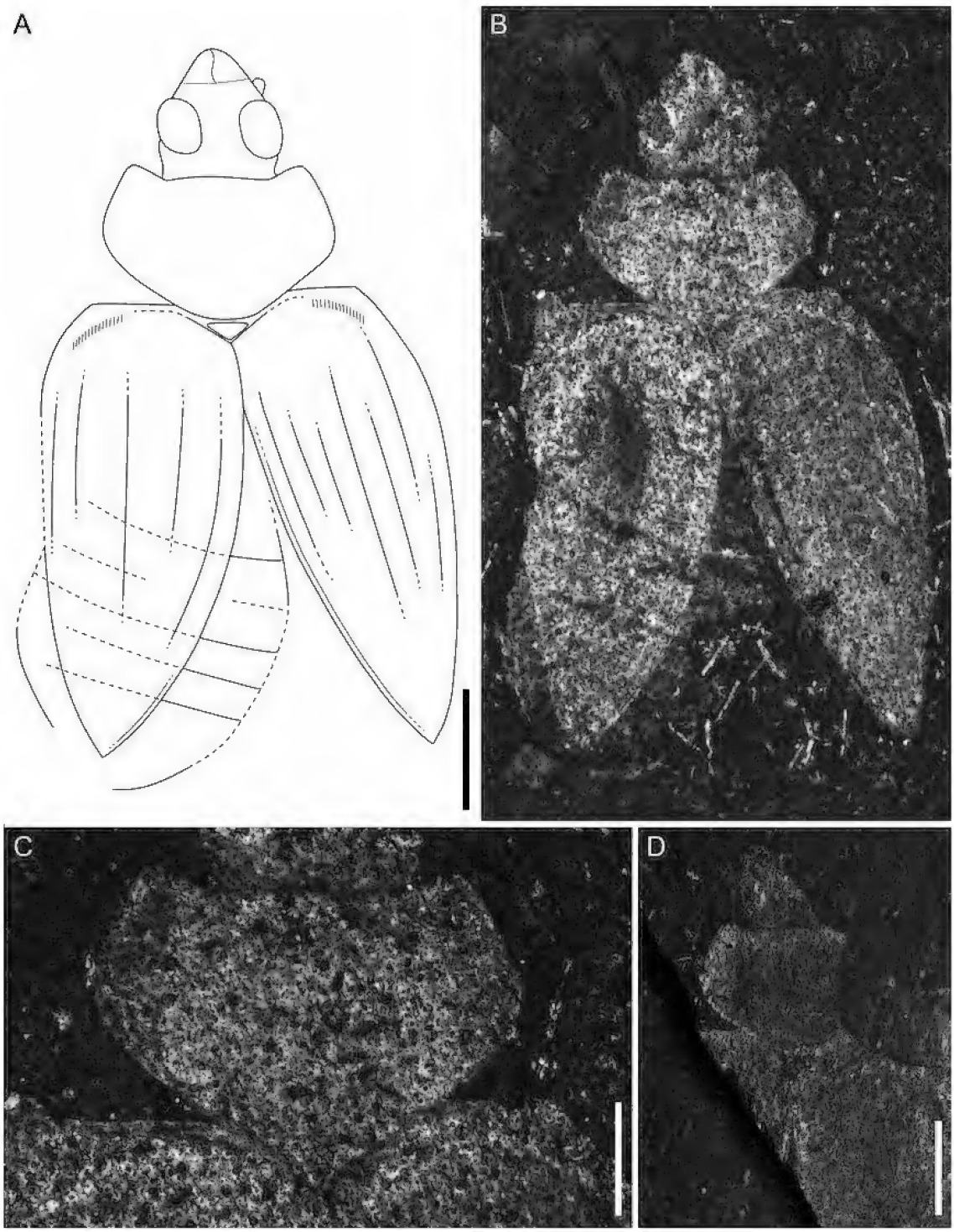

FIG. 52. Morphotype 47. **A, B.** Habitus of VMNH 129485. **C.** Pronotum of VMNH 129485. **D.** Similar specimen, VMNH 97637, possibly belonging to this morphotype. Scale bars: A, B, D: 1 mm; C: 0.5 mm.

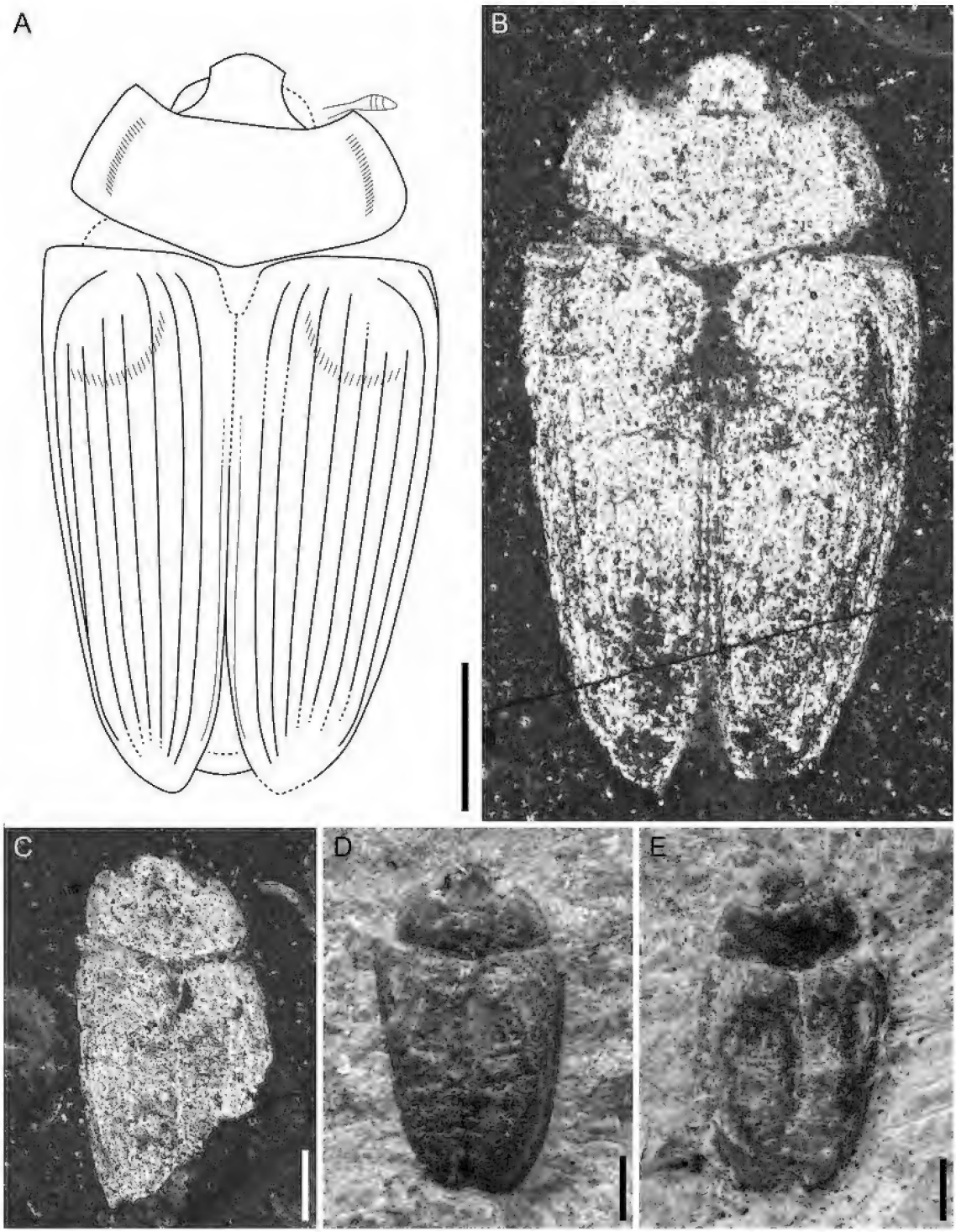

FIG. 53. Morphotype 48. **A, B.** Habitus of VMNH 49781. **C.** Habitus of VMNH 129489. **D, E.** Similar specimens (In.49572, In.64024) from the Lower Liassic of Dorset, England. Photographs courtesy of the Natural History Museum London. Scale bars: 1 mm.

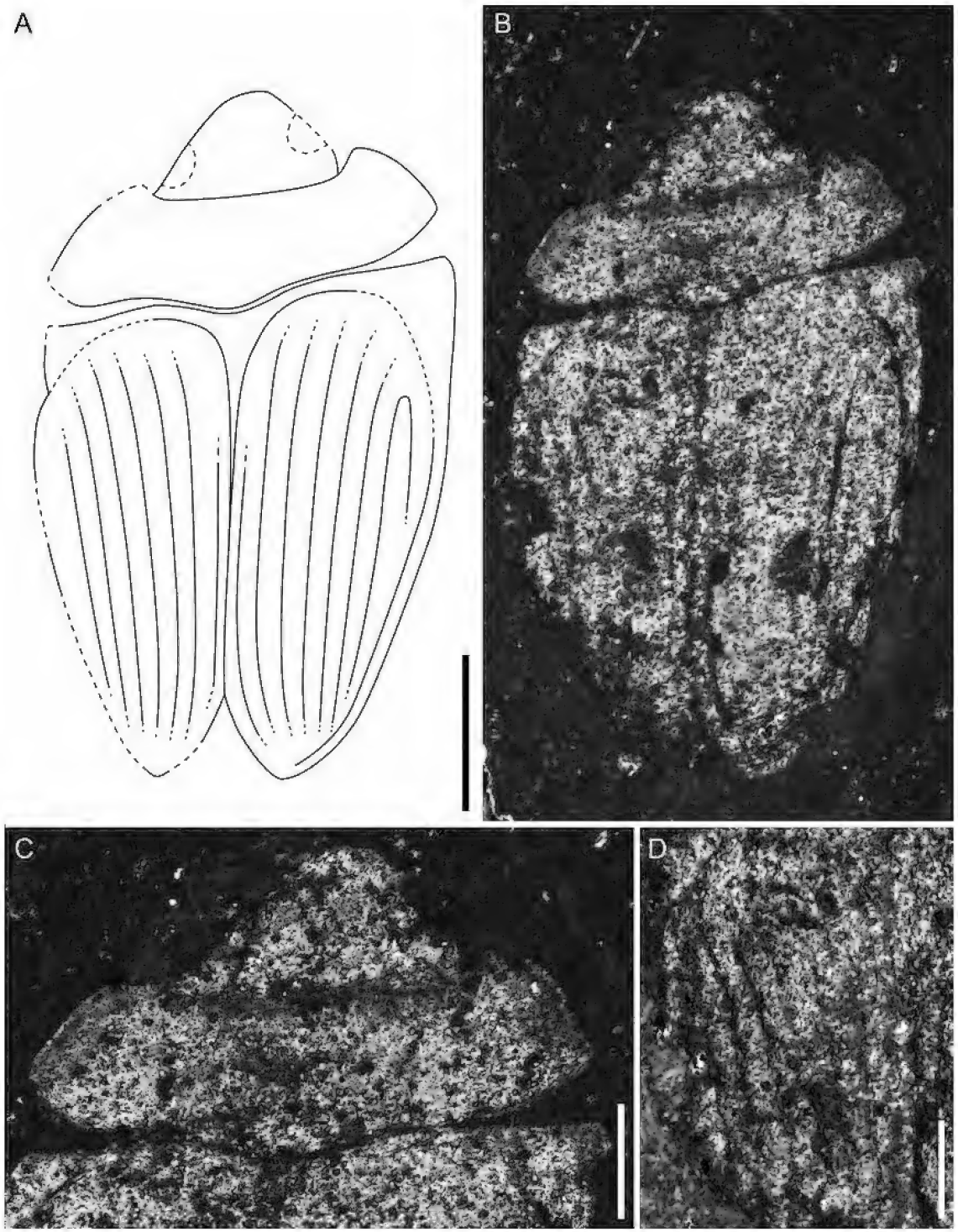

FIG. 54. Morphotype 49, VMNH 53851. **A, B.** Habitus. **C.** Head and pronotum. **D.** Left elytron showing distinct elytral striae. Photograph taken without ethanol and specimen tilted at an angle. Scale bars: A, B: 1 mm; C, D: 0.5 mm.

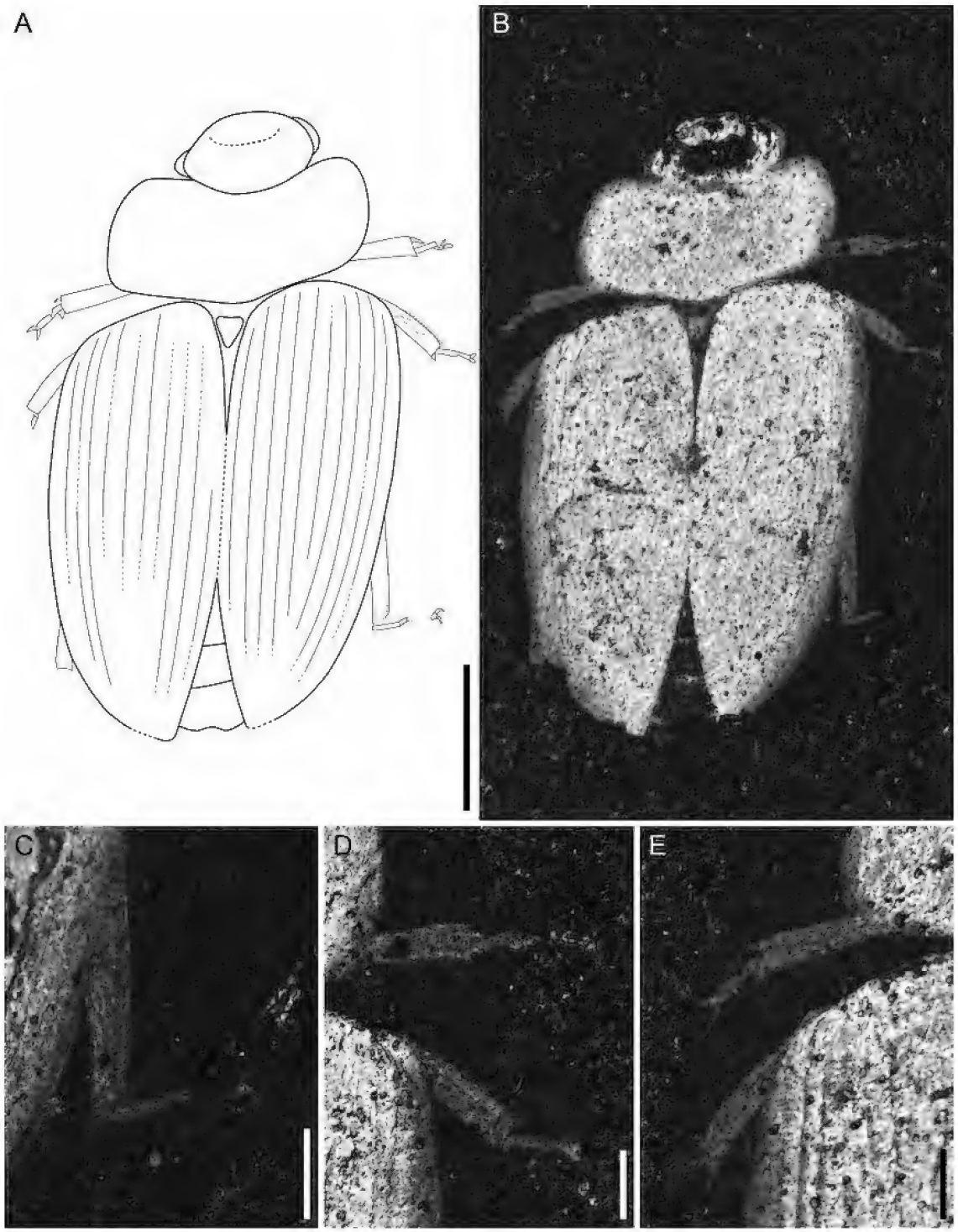

FIG. 55. Morphotype 50, VMNH 49790. **A, B.** Habitus. **C.** Right hind leg. **D.** Right foreleg and middle leg. **E.** Left foreleg and middle leg. Scale bars: A, B: 1 mm; C–E: 0.25 mm.

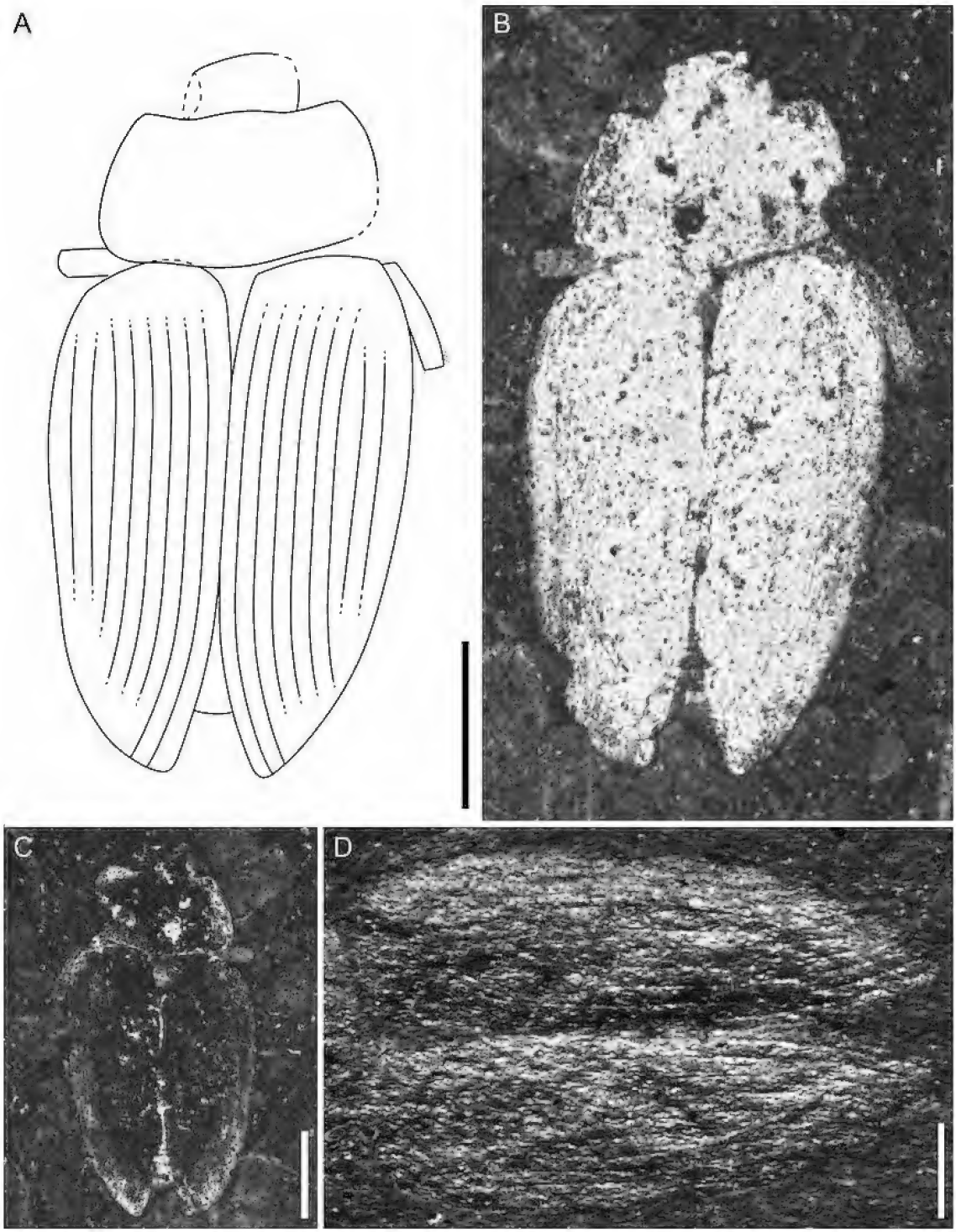

FIG. 56. Morphotype 51, VMNH 51831. **A, B.** Part. **C.** Counterpart. **D.** Elytra of part showing striae. Photograph taken without ethanol and specimen tilted at an angle. Scale bars: A–C: 1 mm; D: 0.5 mm.

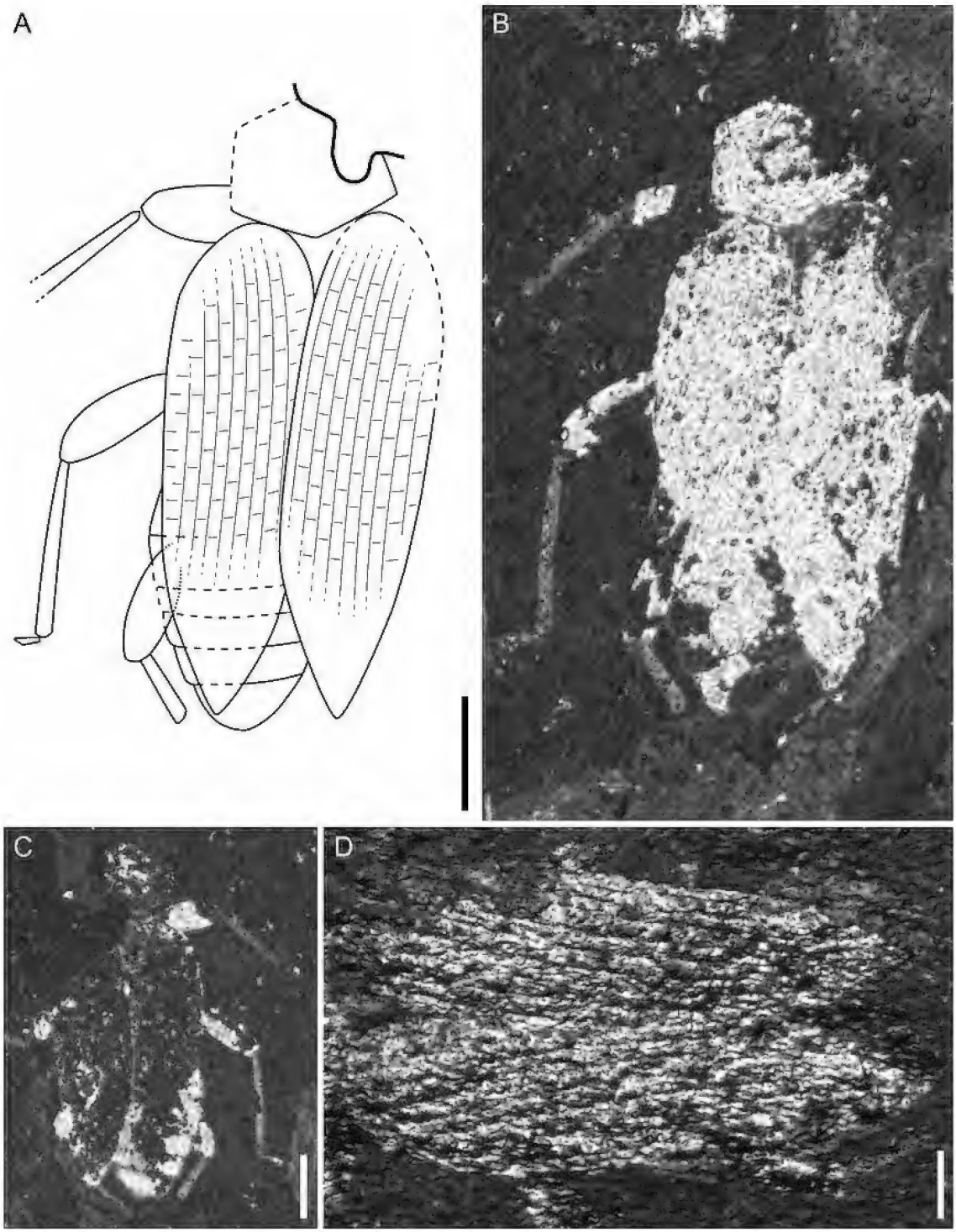

FIG. 57. Morphotype 52. **A, B.** VMNH 51649, part. **C.** VMNH 51651, counterpart. **D.** Elytra of part showing striae. Photograph taken without ethanol and specimen tilted at an angle. Scale bars: A–C: 0.5 mm; D: 0.25 mm.

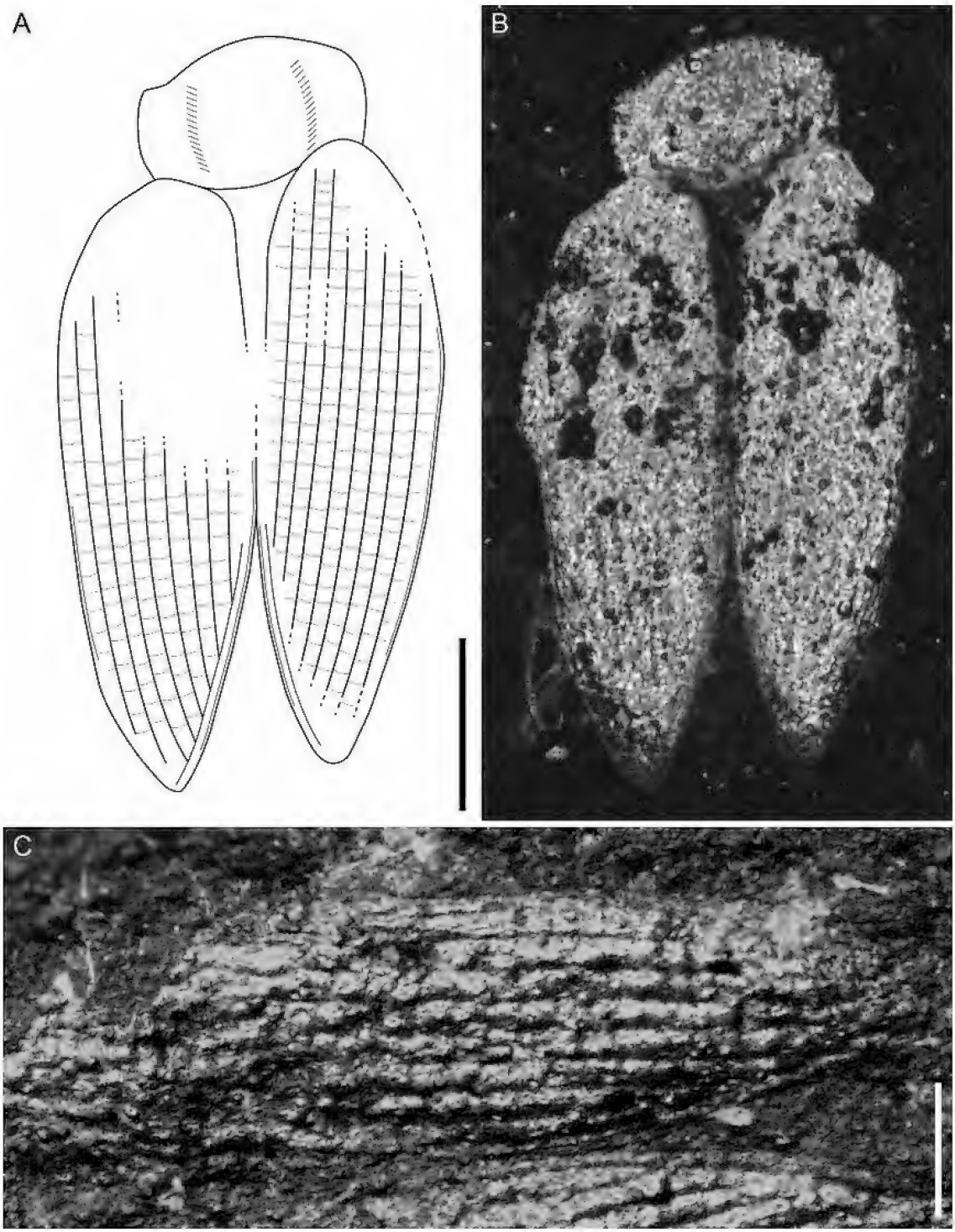

FIG. 58. Morphotype 53, YPM IP 016827. **A, B.** Habitus. **C.** Right elytron showing striae and irregular cells. Photograph taken without ethanol and specimen tilted at an angle. Scale bars: A, B: 0.5 mm; C: 0.25 mm.

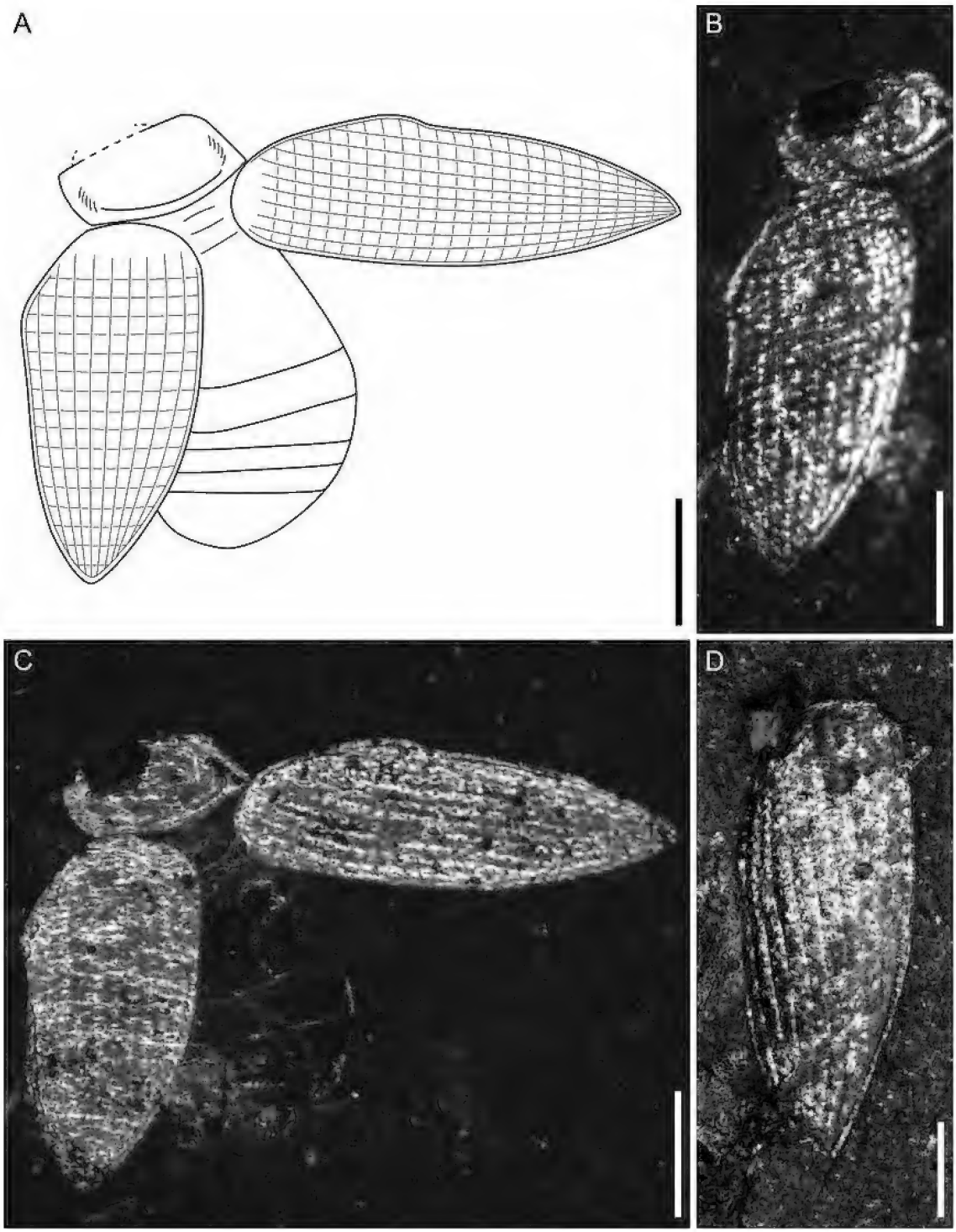

FIG. 59. Morphotype 54. **A, C.** Habitus of VMNH 92751. **B.** Left elytron showing striae and reticulations. Photograph taken without ethanol and specimen tilted at an angle. **D.** Isolated elytron VMNH 97590 (morphotype 98) showing similar reticulations. Scale bars: 0.5 mm.

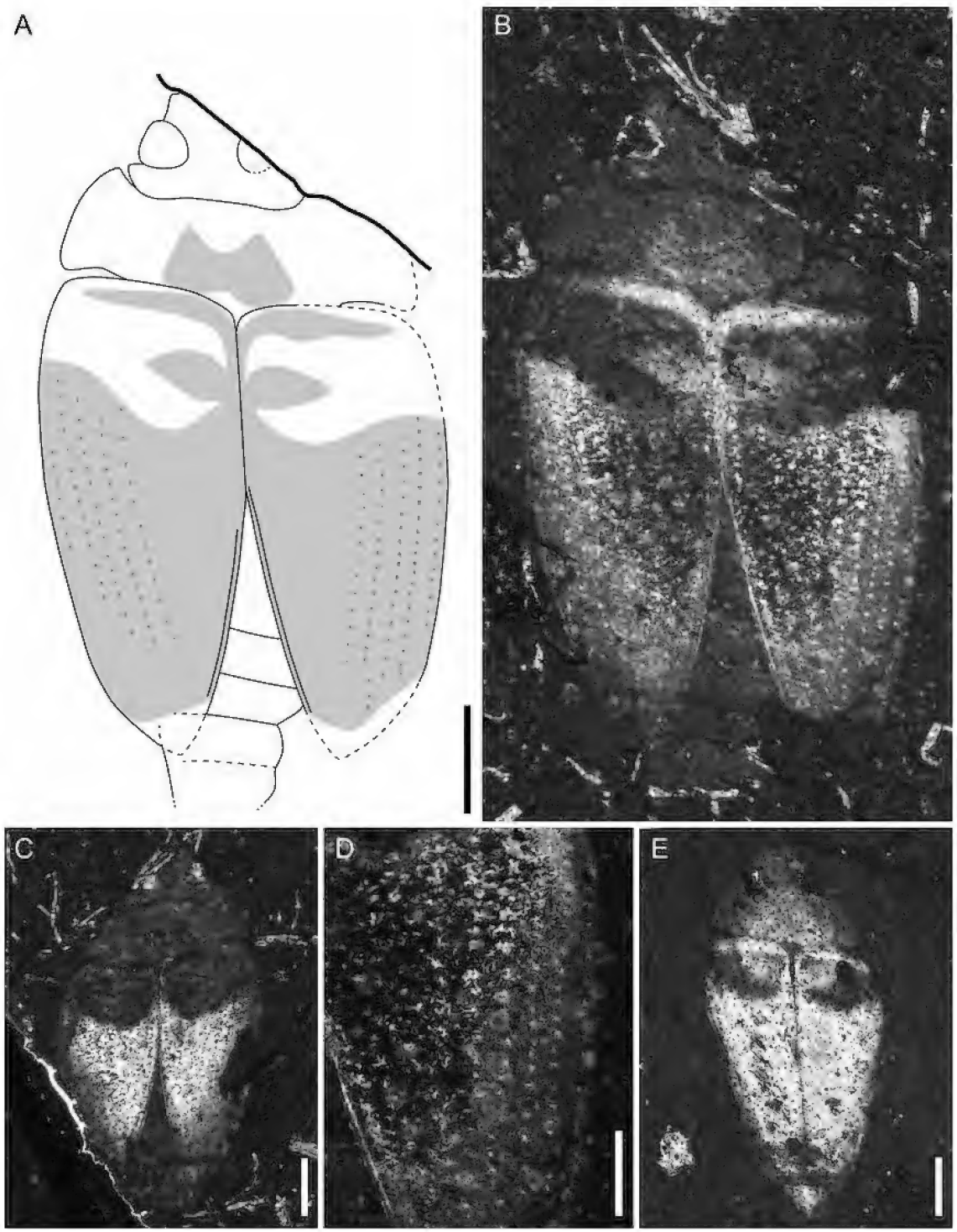

FIG. 60. Morphotype 55. **A, B.** YPM IP 016828, part. **C.** YPM IP 036446, counterpart. **D.** Right elytron of part showing rows of punctures. **E.** VMNH 49762. Scale bars: A–C, E: 0.5 mm; D: 0.25 mm.

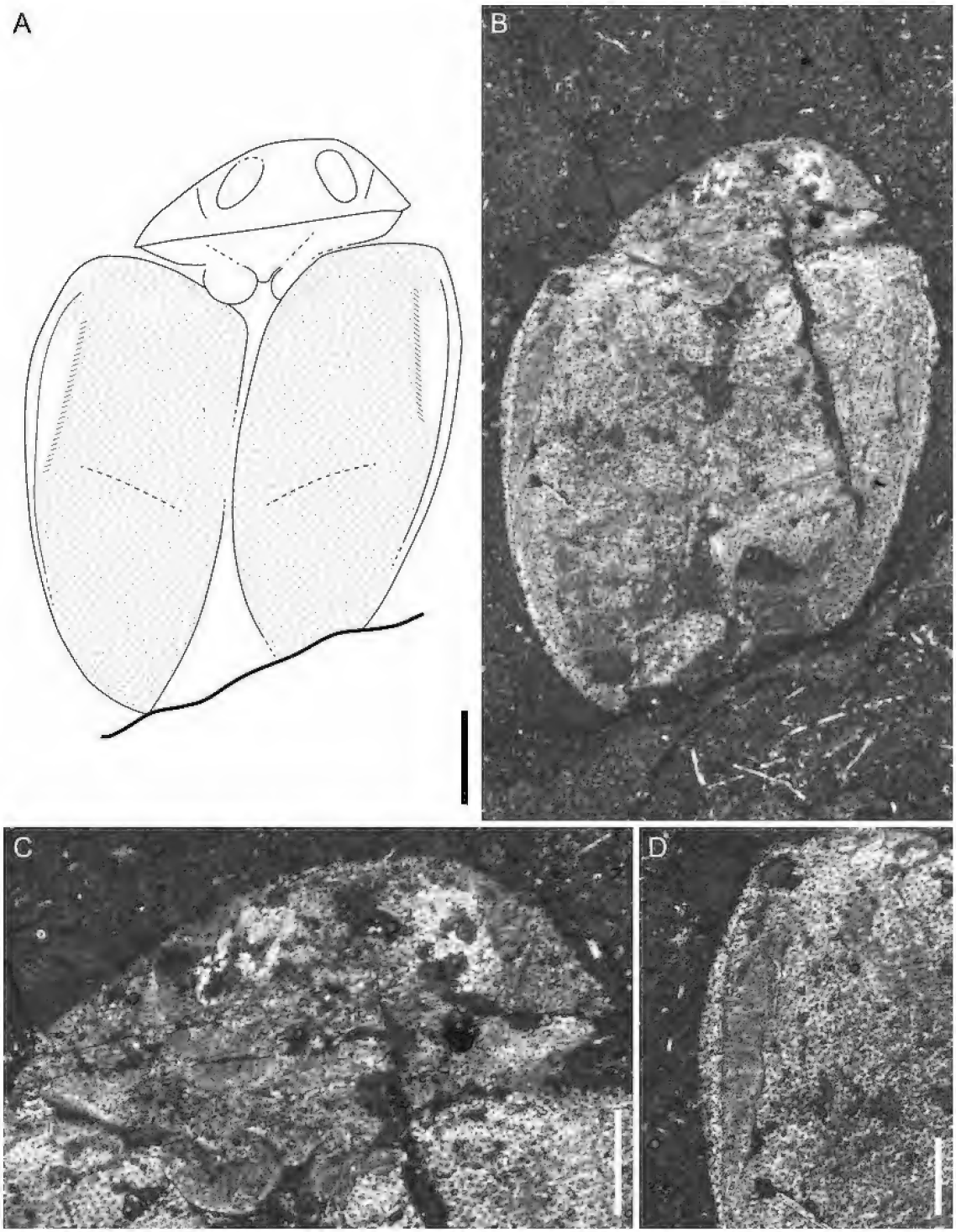

FIG. 61. Morphotype 56, VMNH 129481. **A, B.** Habitus. **C.** Partial head and thorax. **D.** Left elytron showing dense punctures and depressed, anterolateral ledge. Scale bars: A, B: 1 mm; C, D: 0.5 mm.

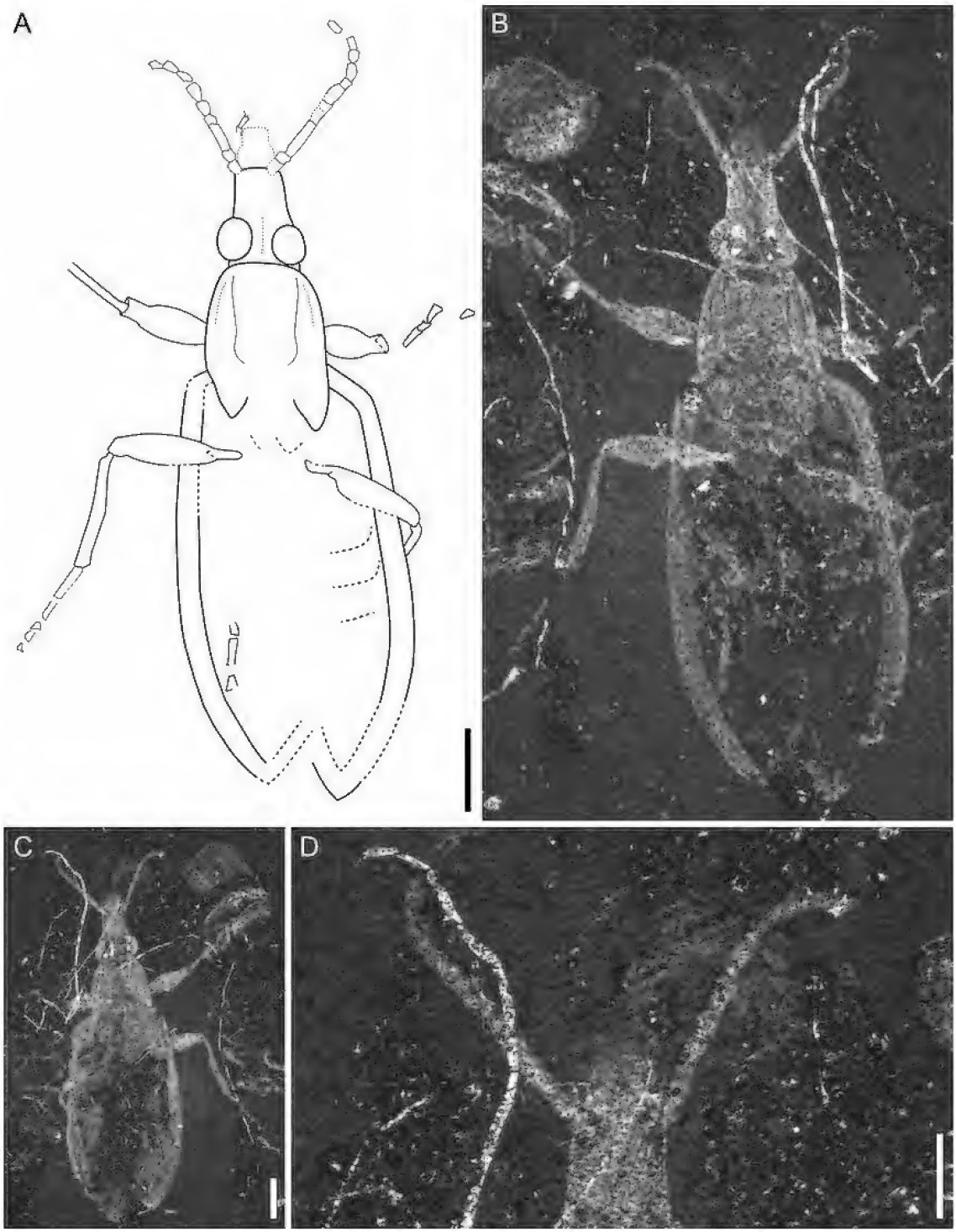

FIG. 62. Morphotype 57, VMNH 97968. **A, B.** Part. **C.** Counterpart. **D.** Antennae and expanded preocular area (head) of counterpart. Scale bars: A–C: 1 mm; D: 0.5 mm.

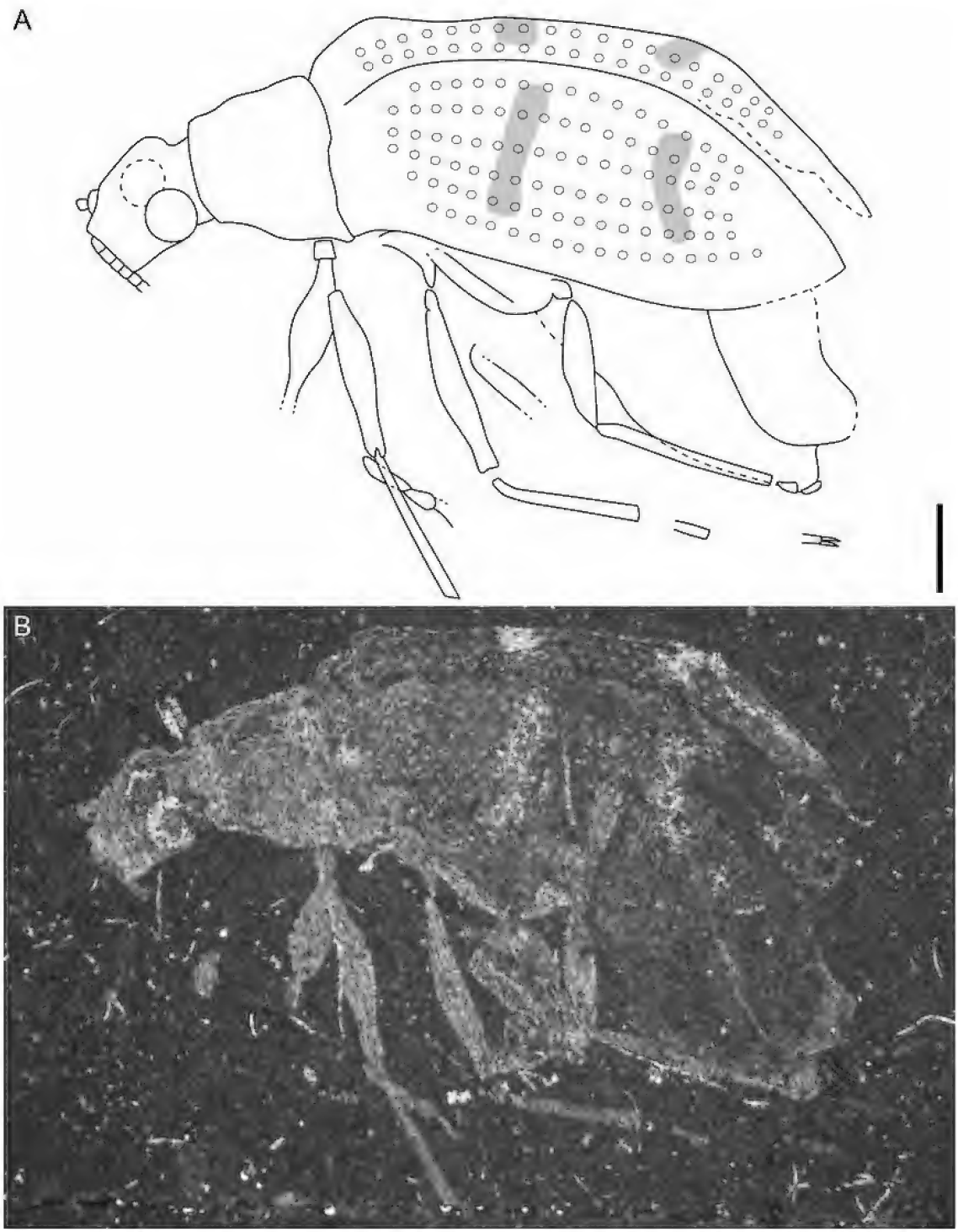

FIG. 63. Morphotype 58, VMNH 92743. Scale bar: 1 mm.

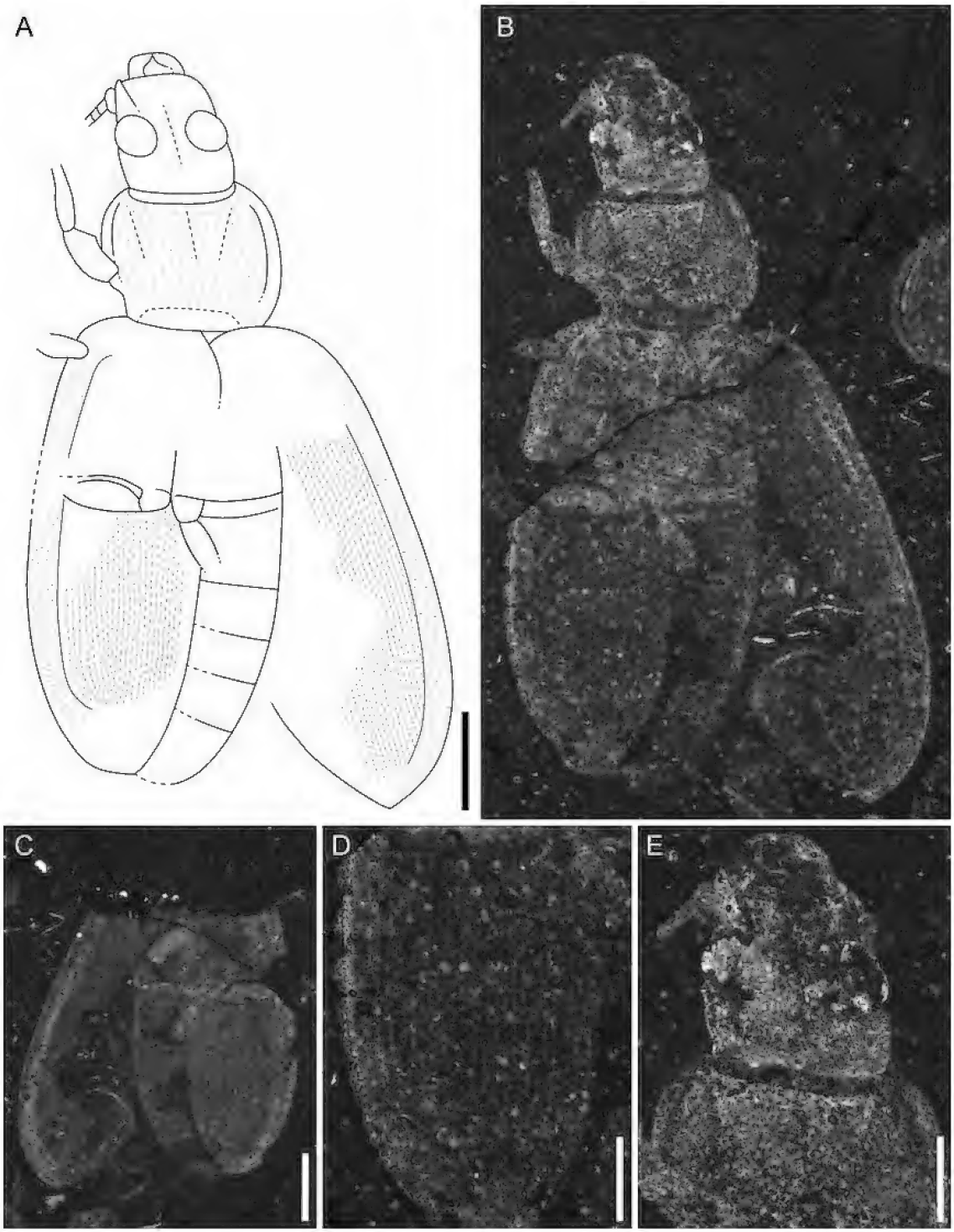

FIG. 64. Morphotype 59, YPM IP 016838. **A, B.** Part. **C.** Counterpart, head not preserved. **D.** Left elytron of part showing rows of fine punctures. **E.** Head and pronotum of part. Scale bars: A–C: 1 mm; D, E: 0.5 mm.

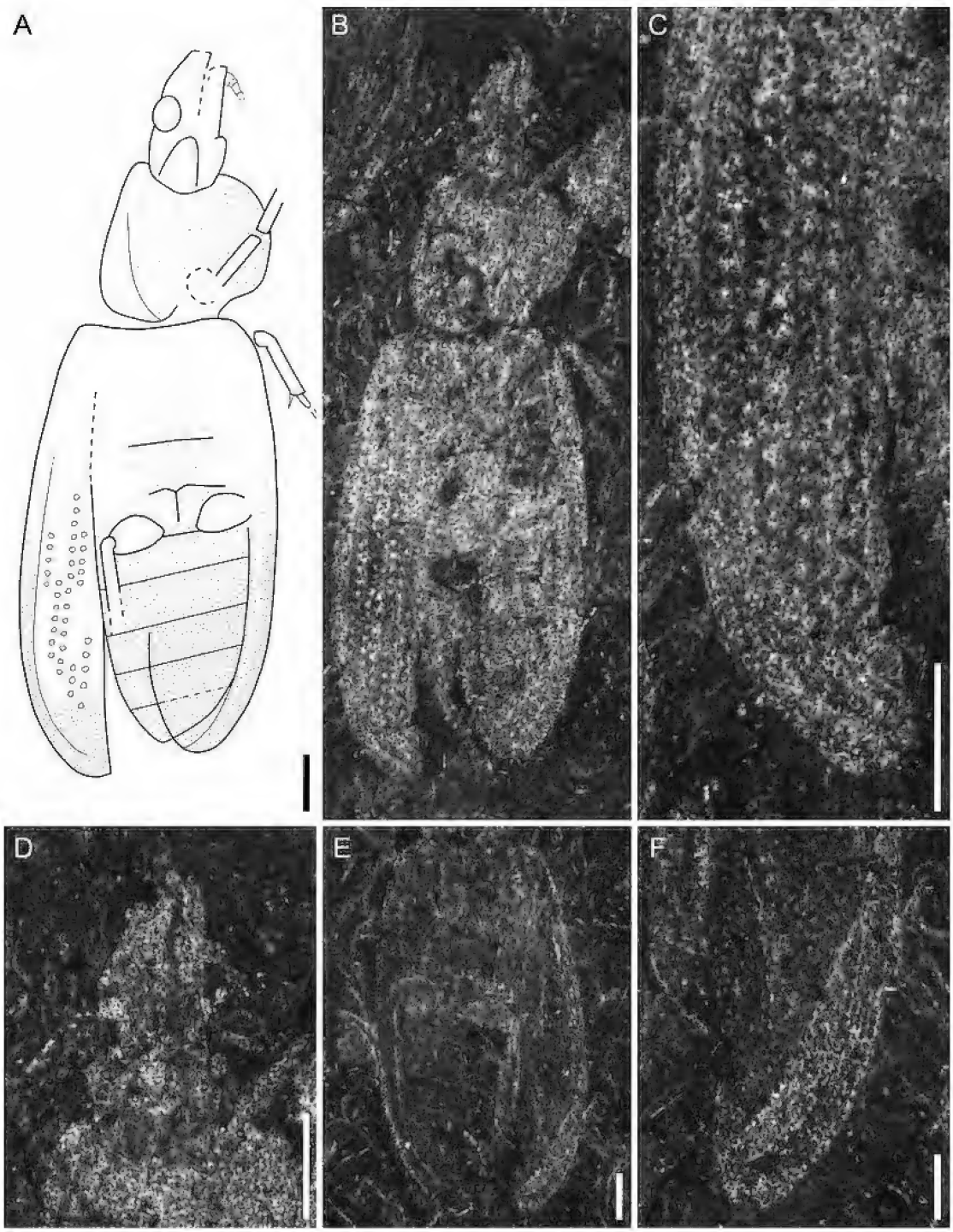

FIG. 65. Morphotype 60, AMNH 04-59. **A, B.** Part. **C.** Left elytron of part showing rows of punctures. **D.** Head of part. **E.** Counterpart, head not preserved. **F.** Elytral apex of counterpart. Scale bars: A–E: 1 mm; F: 0.5 mm.

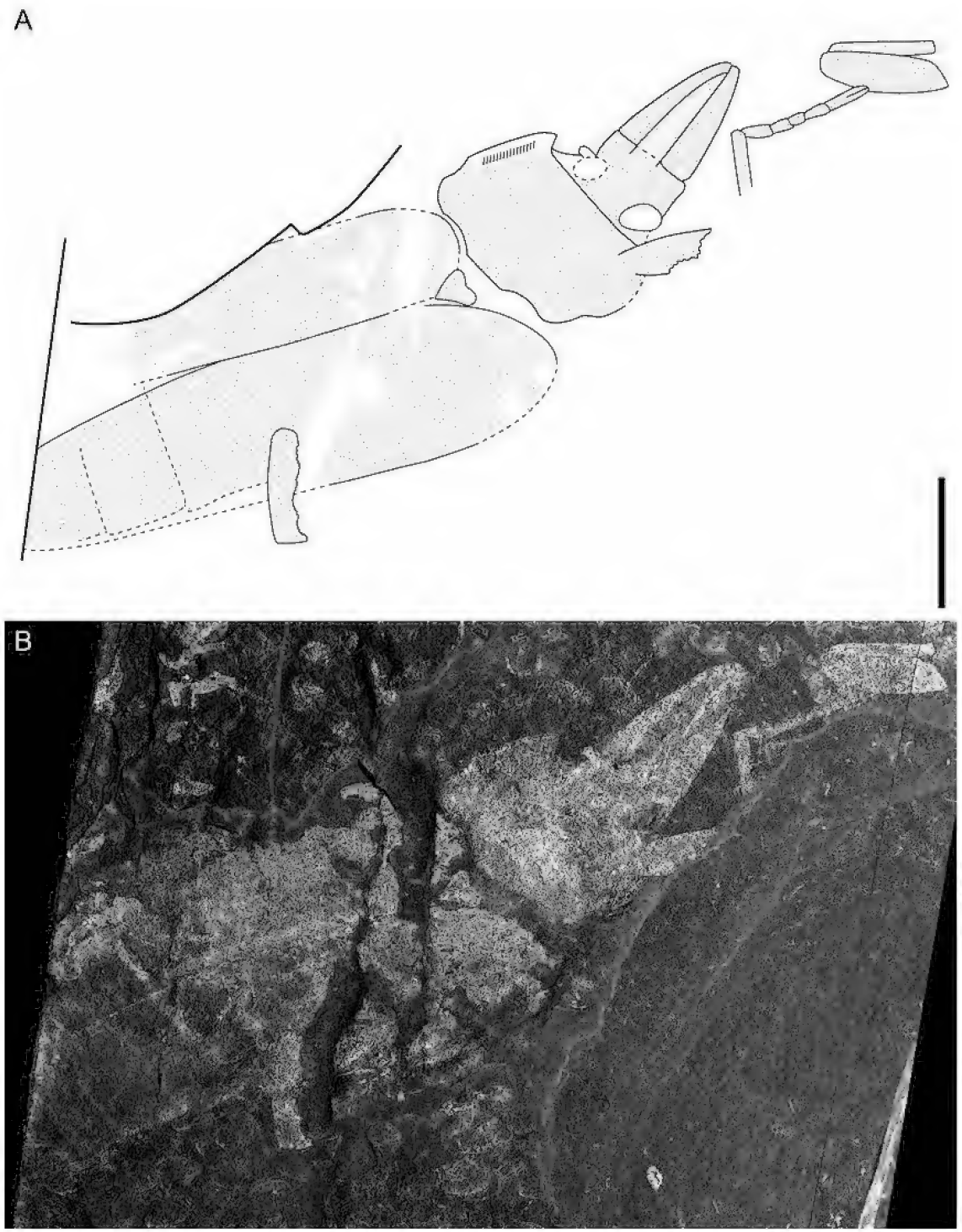

FIG. 66. Morphotype 61, VMNH 49597. **A, B.** Part. Scale bar: 5 mm.

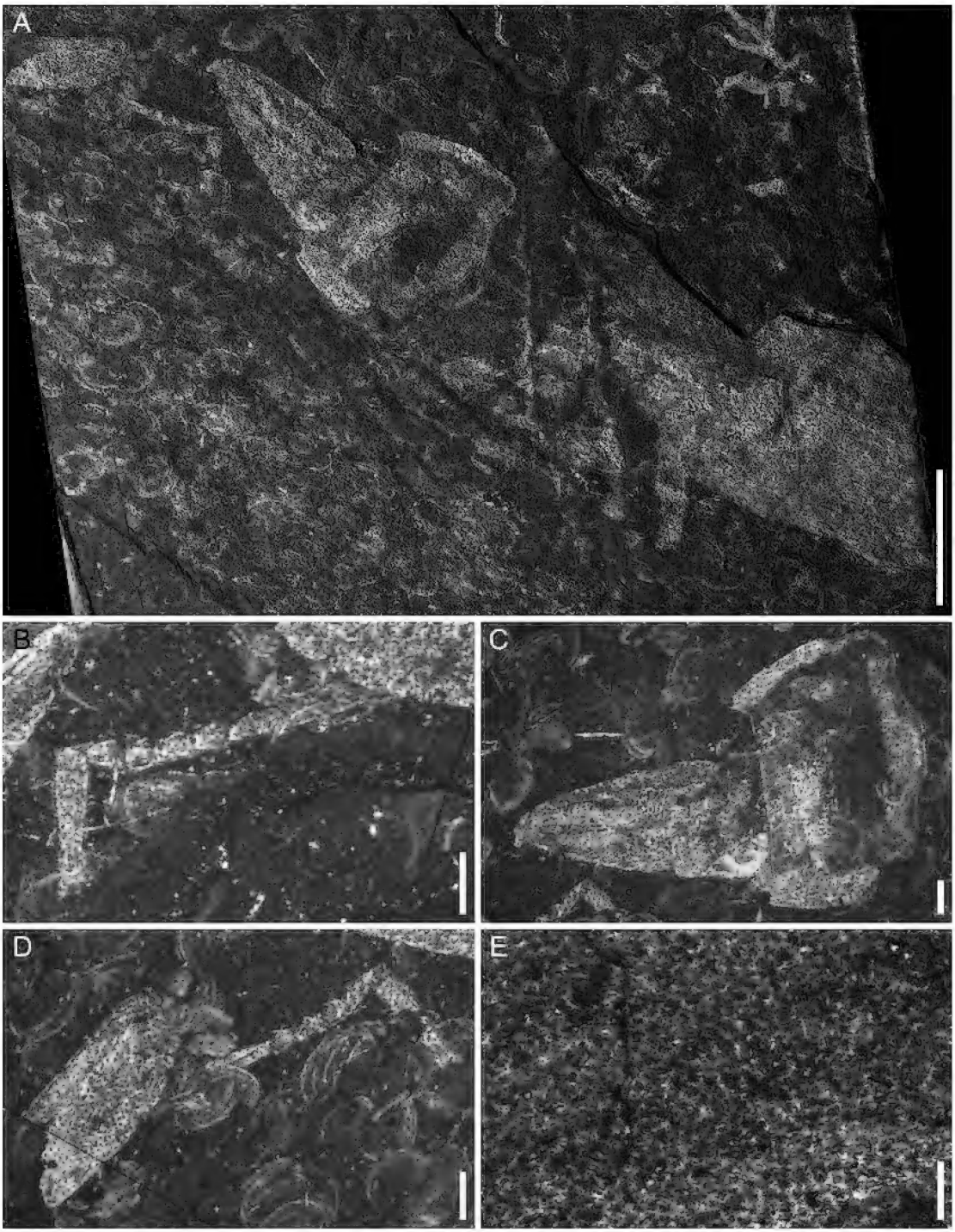

FIG. 67. Morphotype 61, VMNH 49597. **A.** Counterpart. **B.** Foreleg of part. **C.** Head of counterpart. **D.** Foreleg of counterpart showing bilobed segment. **E.** Elytron covered in dense, fine nodules. Scale bars: A: 5 mm; B–D: 1 mm; E: 0.5 mm.

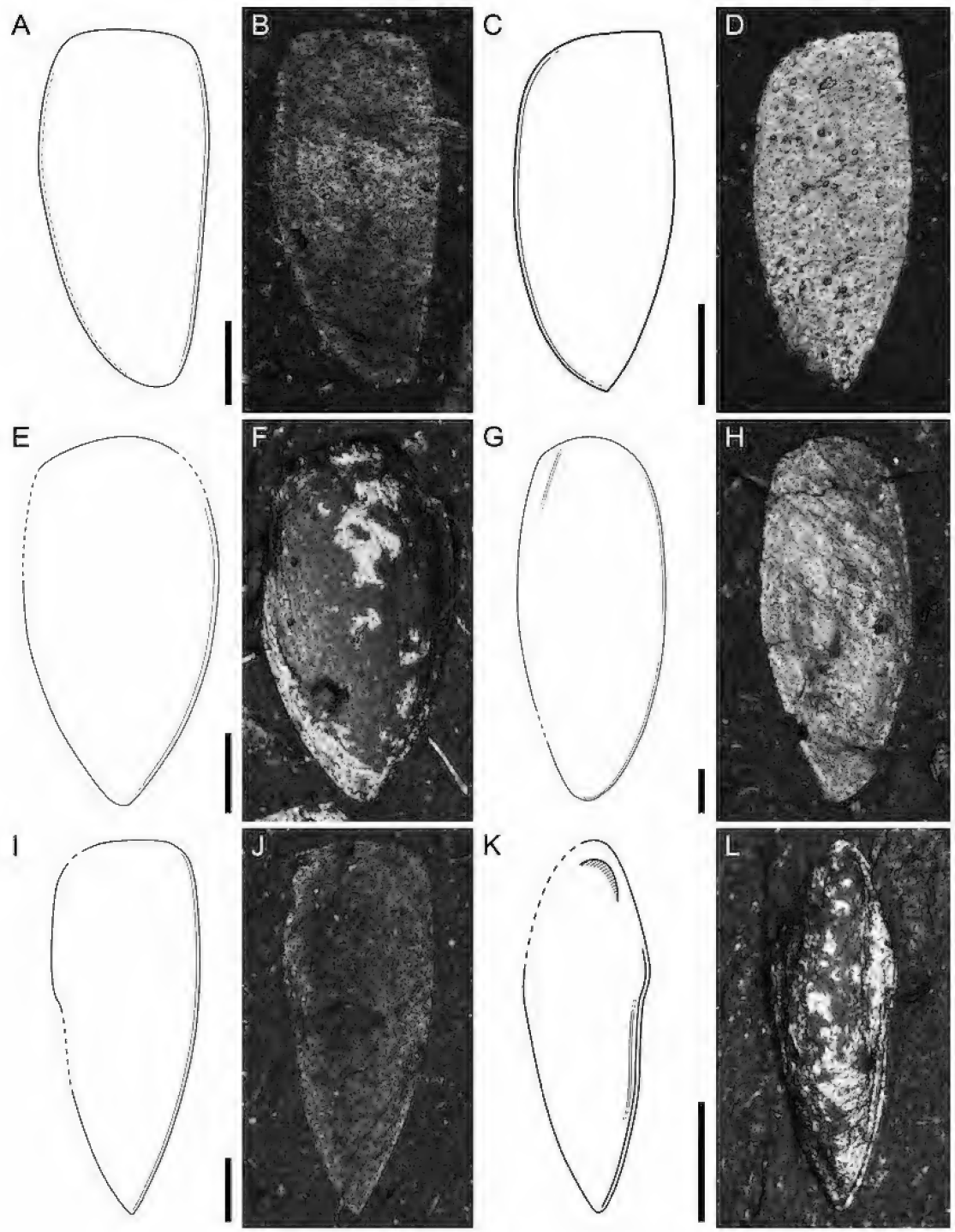

FIG. 68. Smooth elytral morphotypes. **A, B.** Morphotype 62, VMNH 97505. **C, D.** Morphotype 63, VMNH 99030. **E, F.** Morphotype 64, VMNH 95504. **G, H.** Morphotype 65, VMNH 97607. **I, J.** Morphotype 66, VMNH 97319. **K, L.** Morphotype 67, VMNH 97104. Scale bars: 0.5 mm.

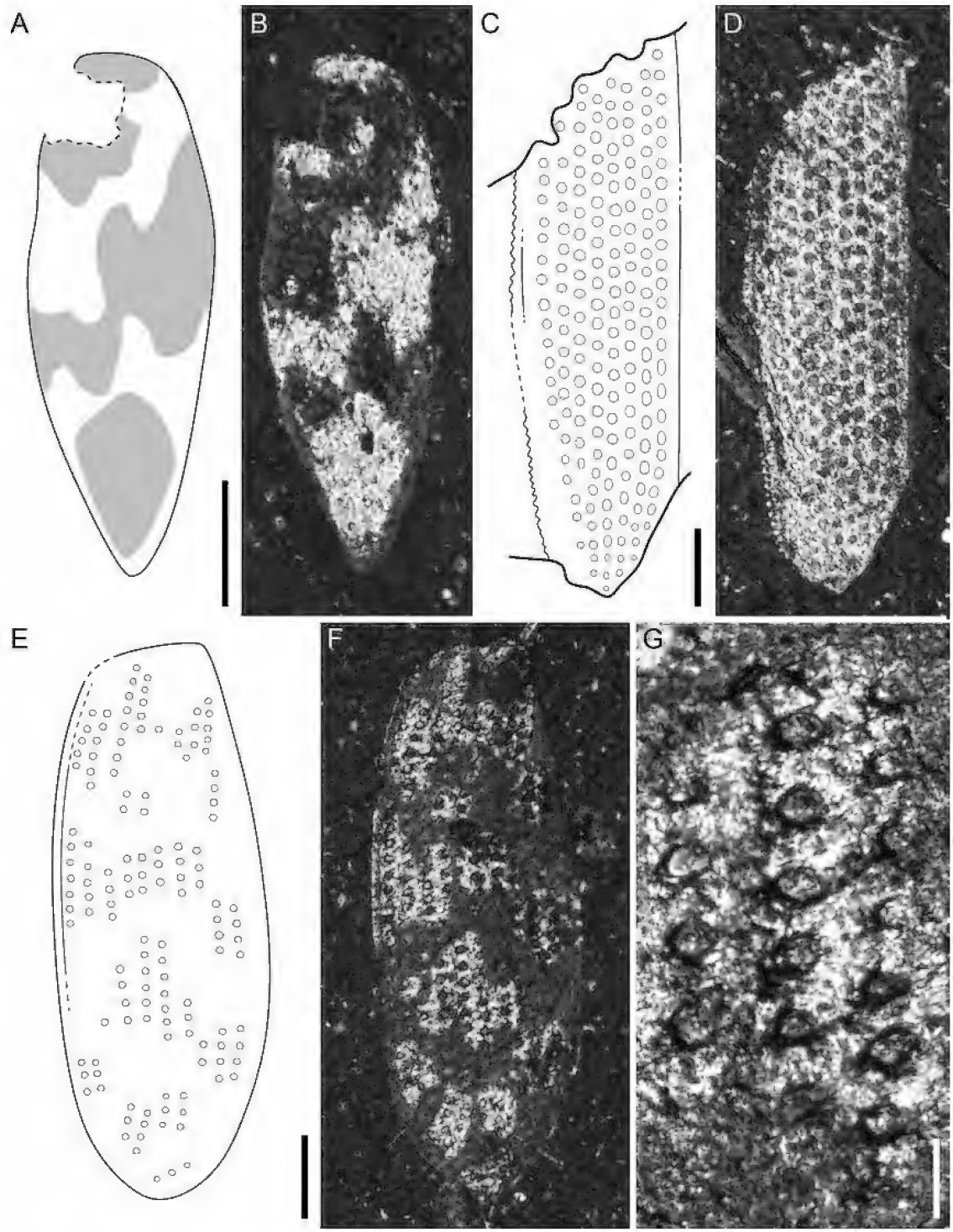

FIG. 69. Elytral morphotypes with color patterns and nodules. **A, B.** Morphotype 68, VMNH 54567. **C, D.** Morphotype 69, VMNH 95448. **E–G.** Morphotype 70, VMNH 95487. Scale bars: A–F: 0.5 mm, G: 0.1 mm.

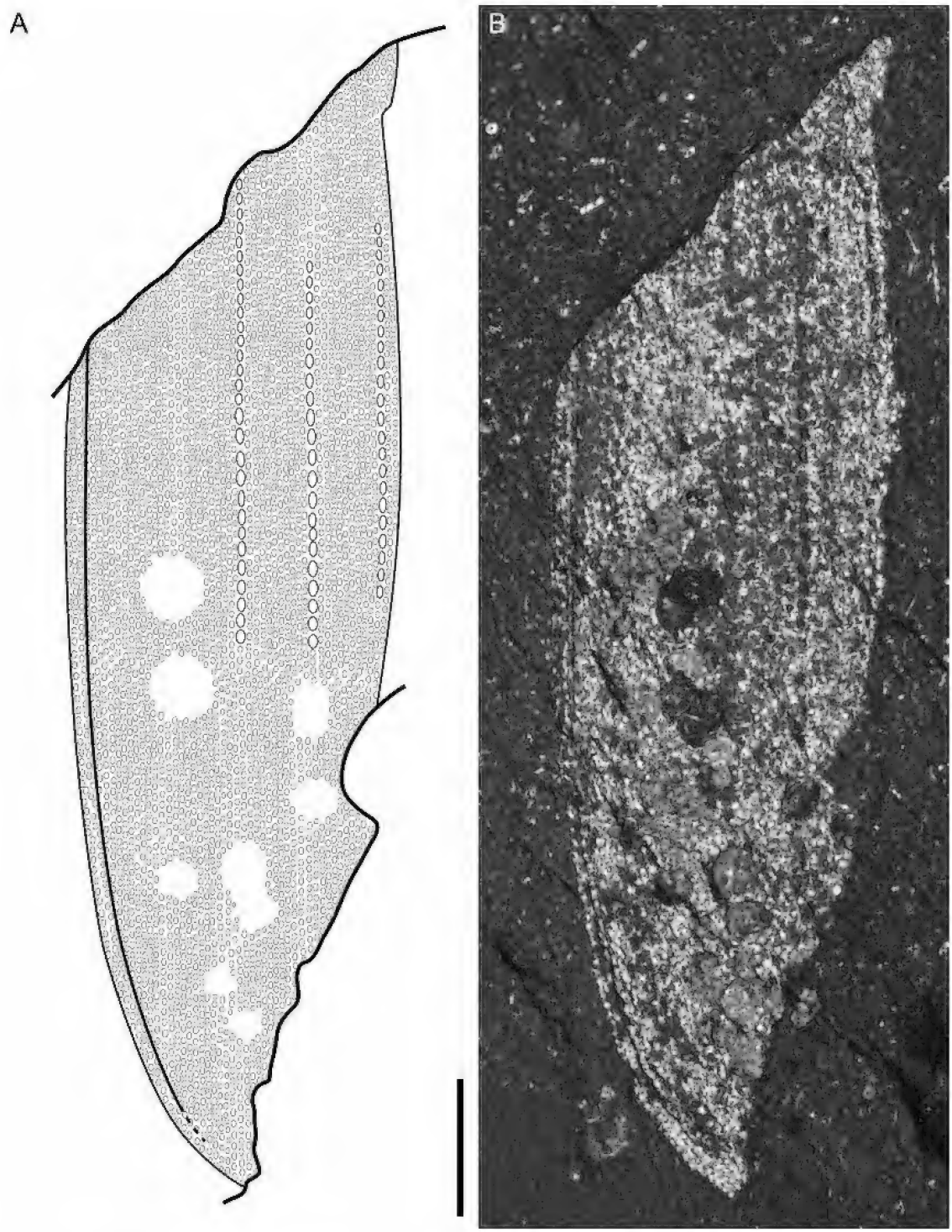

FIG. 70. Nodular elytral morphotype 71, VMNH 97492. Scale bar: 1 mm.

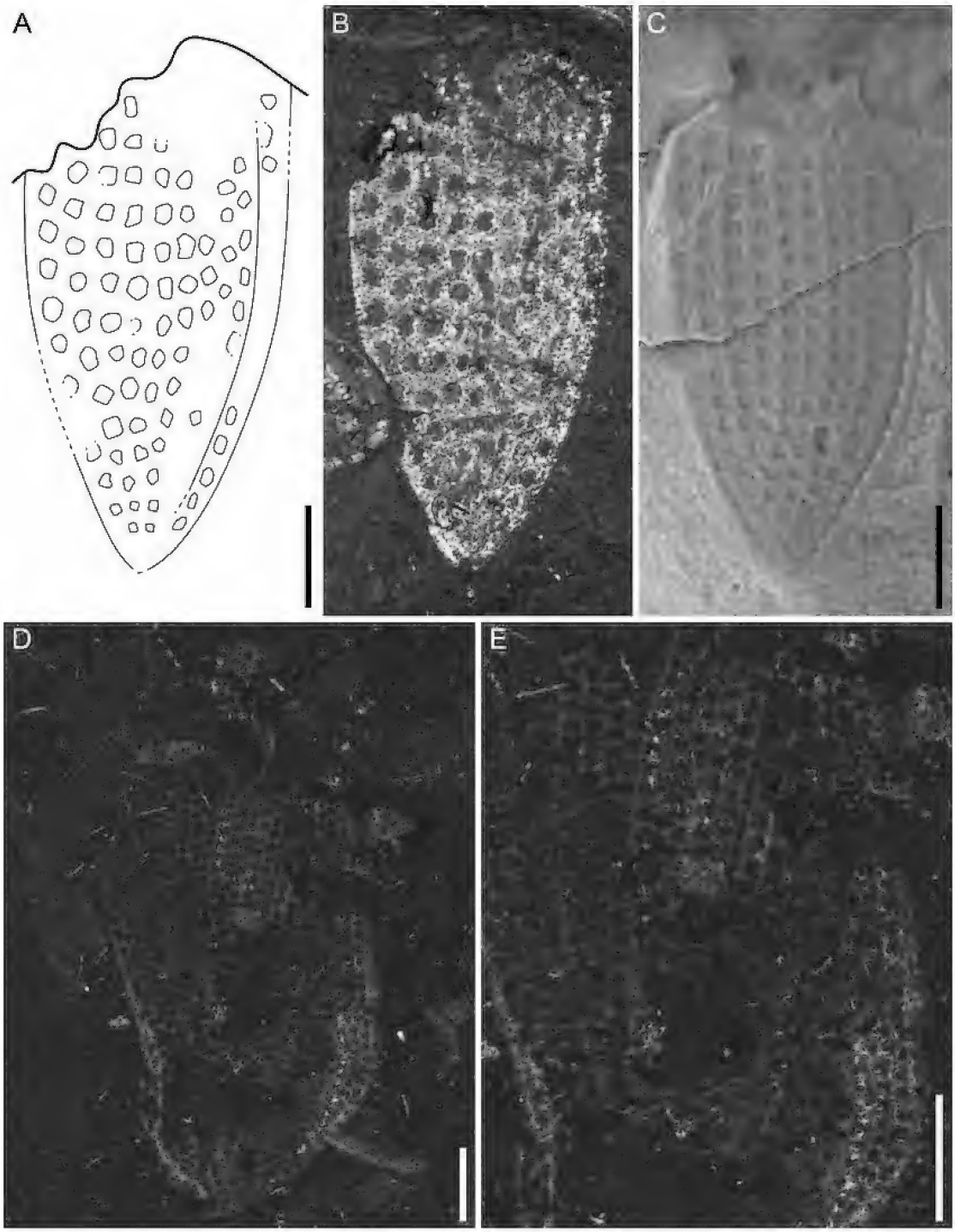

FIG. 71. Elytral morphotypes with window punctures. **A, B.** Morphotype 72, VMNH 49731. **C.** *Zygadenia westraliensis* (E. Jurassic, Western Australia; Martin, 2010). Photo courtesy of Sarah Martin. **D, E.** Morphotype 73, VMNH 94836. Photo courtesy of VMNH. Scale bars: 1 mm.

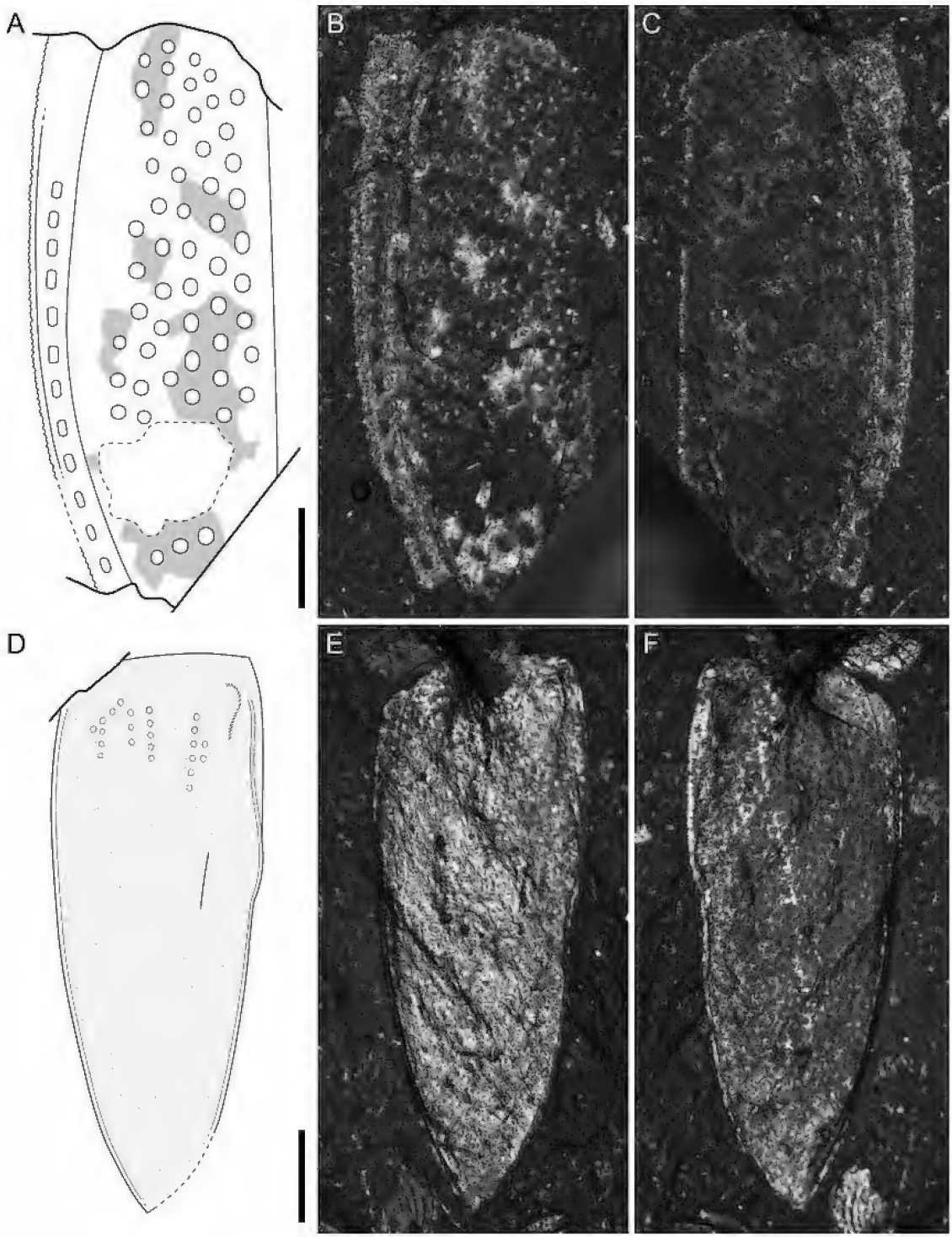

FIG. 72. Punctate elytral morphotypes. **A–C.** Morphotype 74, VMNH 97509. **D–F.** Morphotype 75, VMNH 97500. Scale bars: 1 mm.

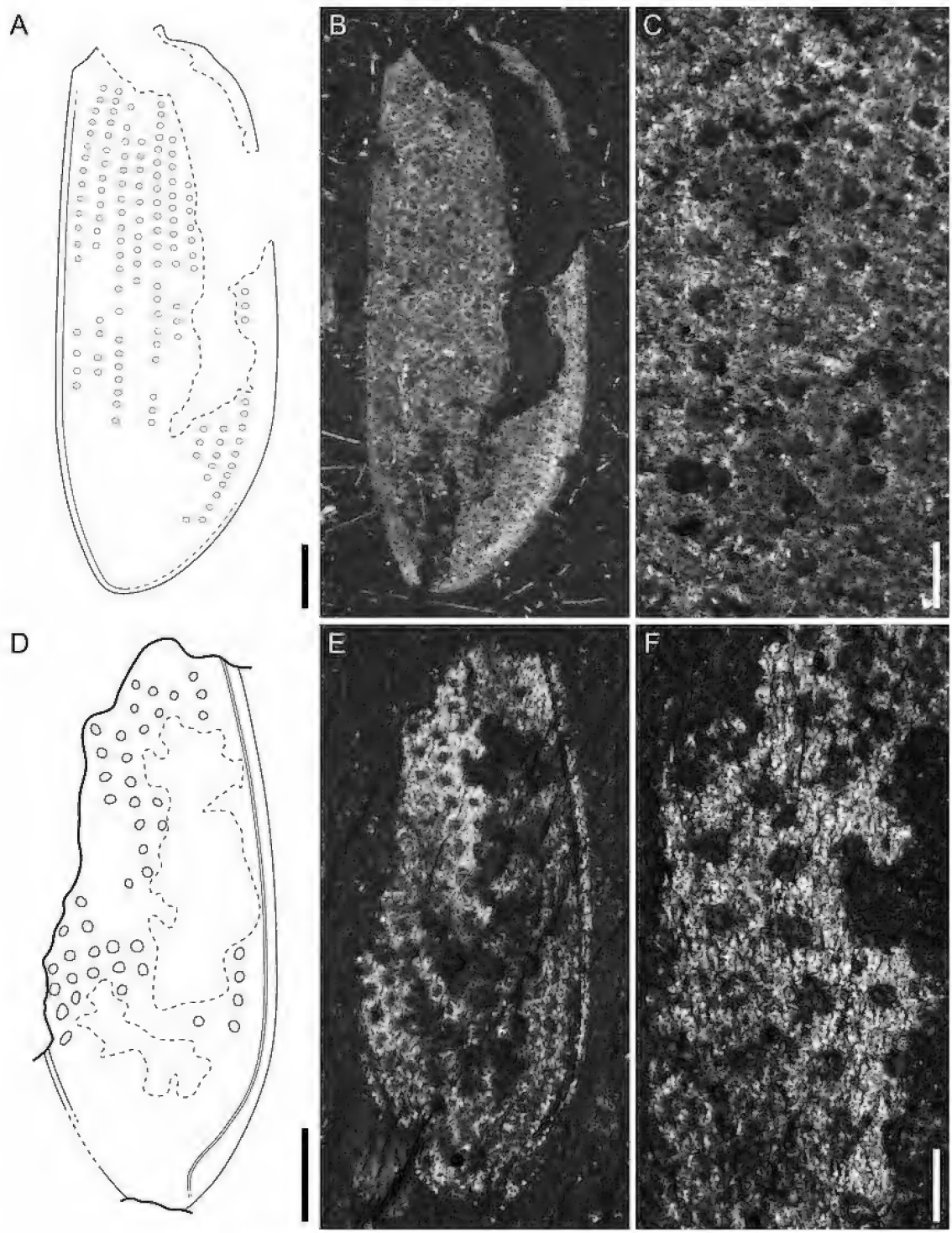

FIG. 73. Punctate elytral morphotypes. **A–C.** Morphotype 76, AMNH 04-87. **D–F.** Morphotype 77, VMNH 97571. Scale bars: A, B, D, E: 1 mm; C, F: 0.25 mm.

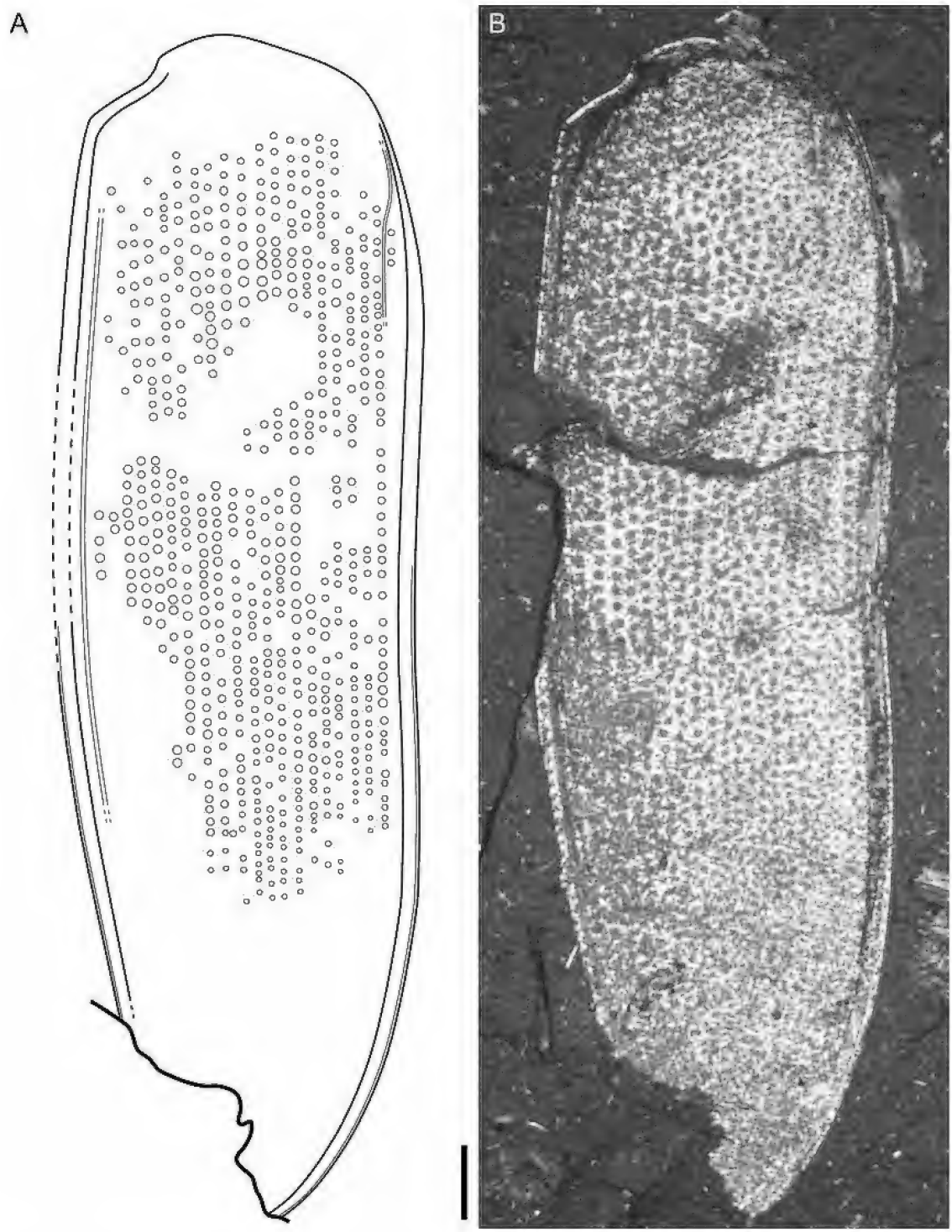

FIG. 74. Punctate elytral morphotype 78, VMNH 95456. Scale bar: 1 mm.

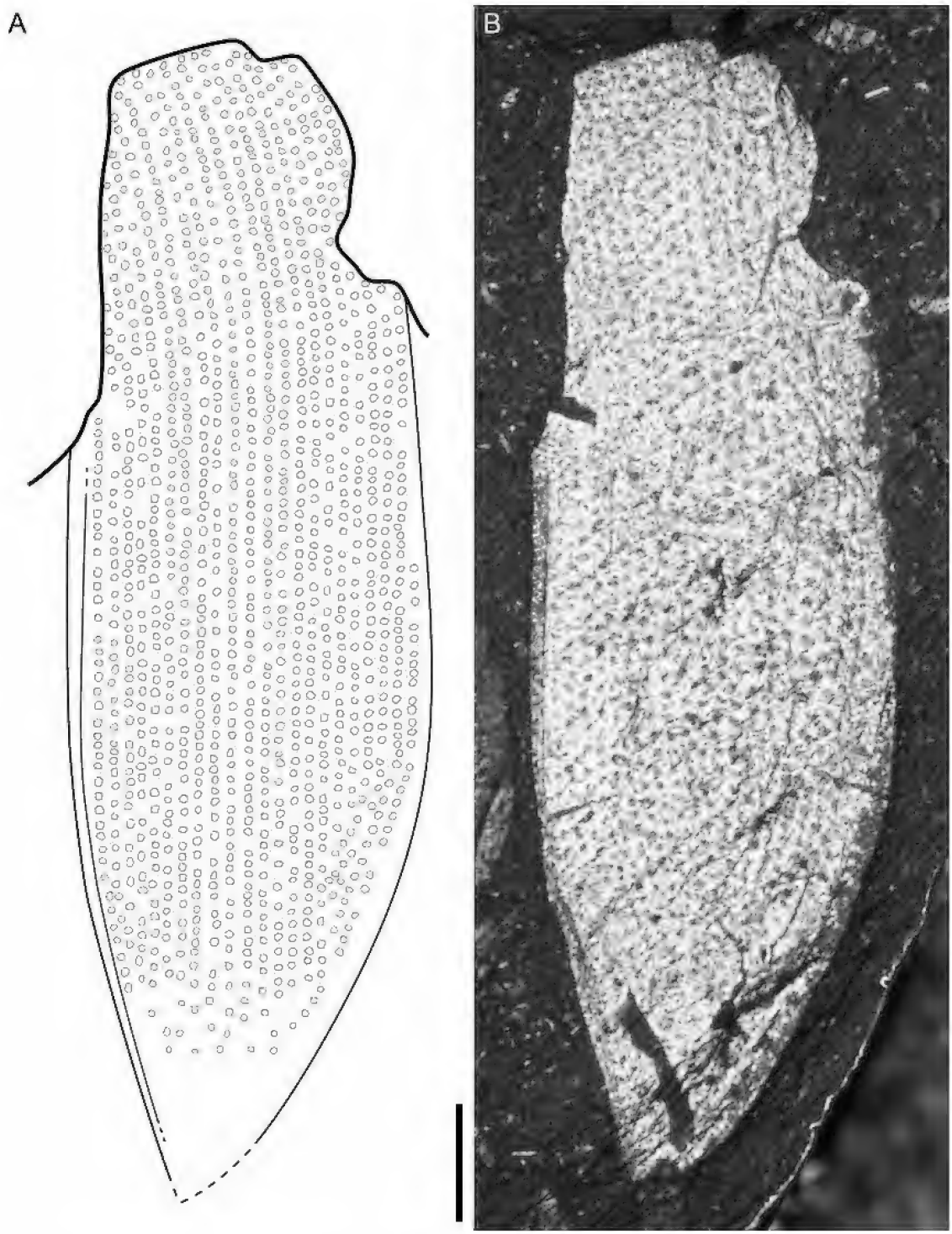

FIG. 75. Punctate elytral morphotype 79, VMNH 97425. Scale bar: 1 mm.

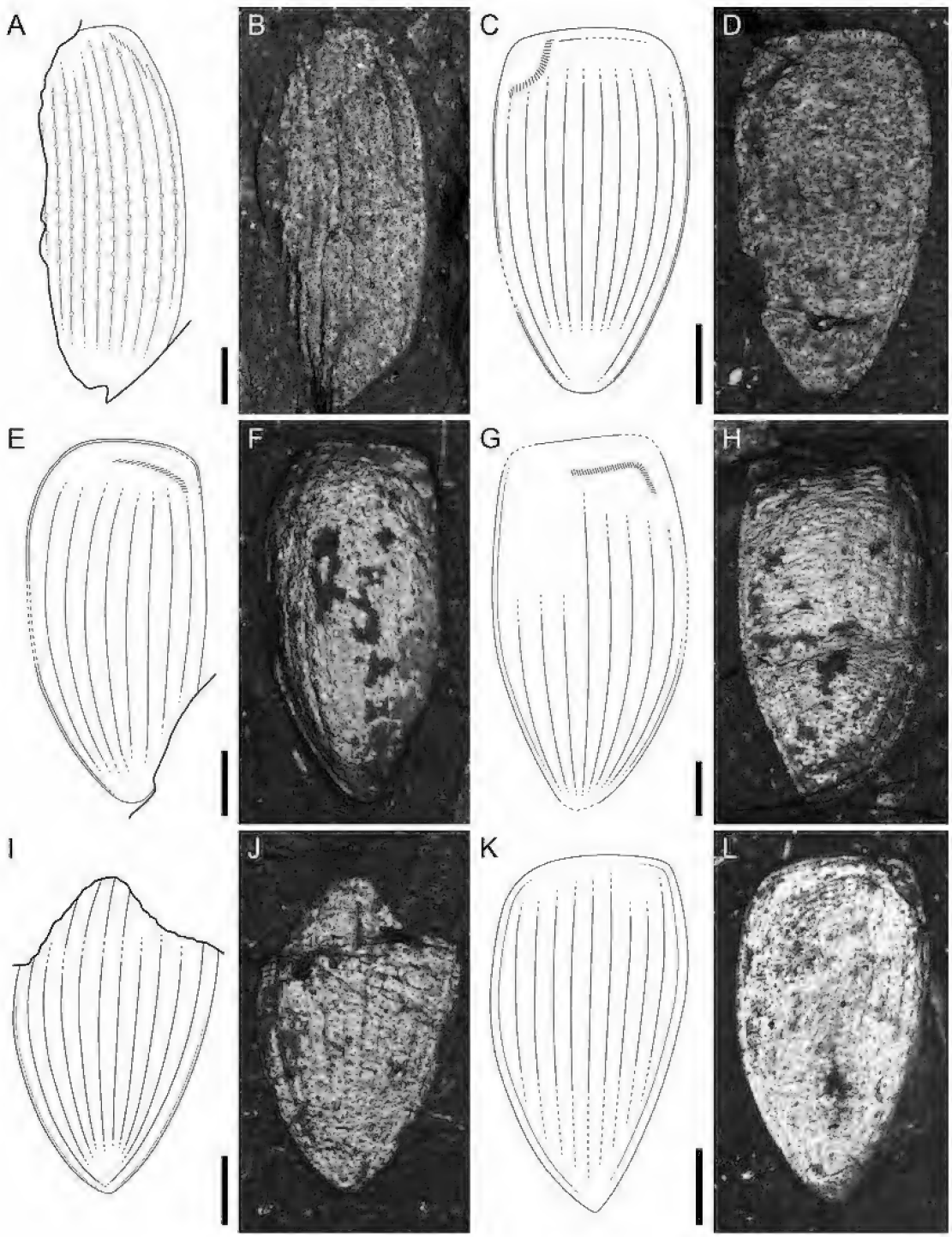

FIG. 76. Striate elytral morphotypes. **A, B.** Morphotype 80, VMNH 95483. **C, D.** Morphotype 81, VMNH 95443. **E, F.** Morphotype 82, VMNH 96665. **G, H.** Morphotype 83, VMNH 96826. **I, J.** Morphotype 84, VMNH 97581. **K, L.** Morphotype 85, VMNH 54201. Scale bars: 0.5 mm.

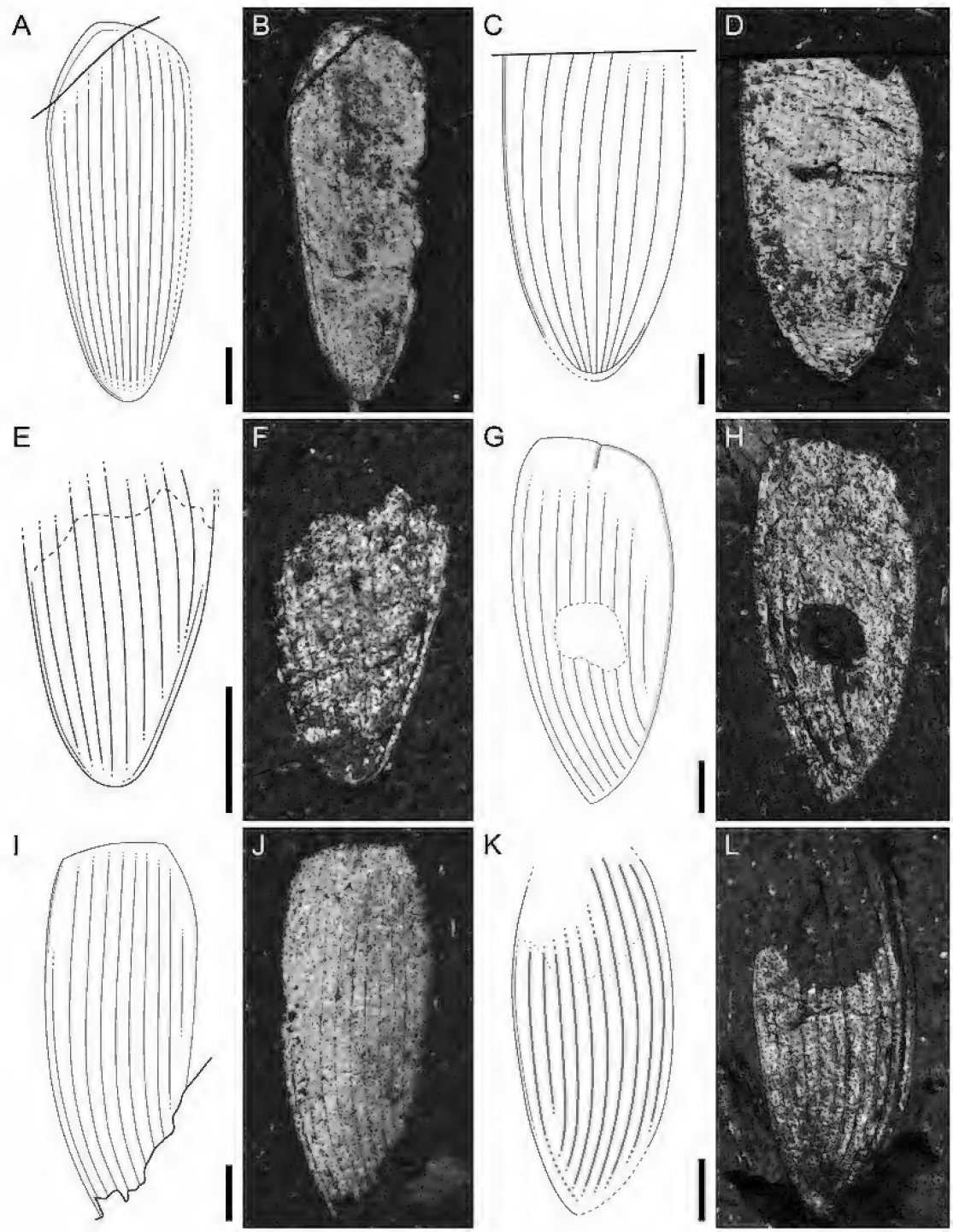

FIG. 77. Striate elytral morphotypes. **A, B.** Morphotype 86, VMNH 50186. **C, D.** Morphotype 87, VMNH 97304. **E, F.** Morphotype 88, VMNH 97376. **G, H.** Morphotype 89, VMNH 98968. **I, J.** Morphotype 90, VMNH 129483. **K, L.** Morphotype 91, VMNH 97346. Scale bars: 0.5 mm.

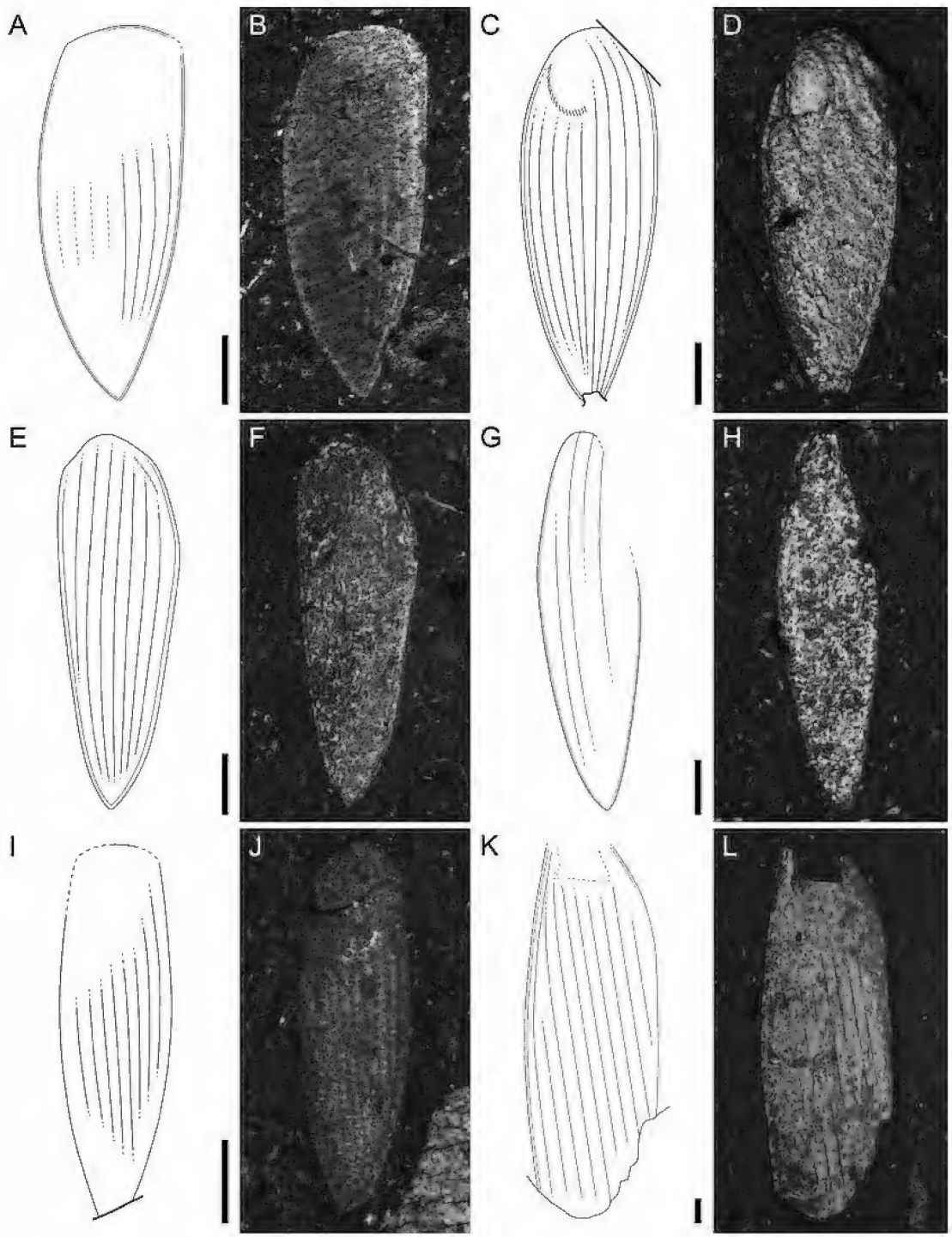

FIG. 78. Striate elytral morphotypes. **A, B.** Morphotype 92, VMNH 95536. **C, D.** Morphotype 93, VMNH 97305. **E, F.** Morphotype 94, VMNH 97583. **G, H.** Morphotype 95, VMNH 98277. **I, J.** Morphotype 96, VMNH 95971. **K, L.** Morphotype 97, VMNH 96824. Scale bars: 0.5 mm.

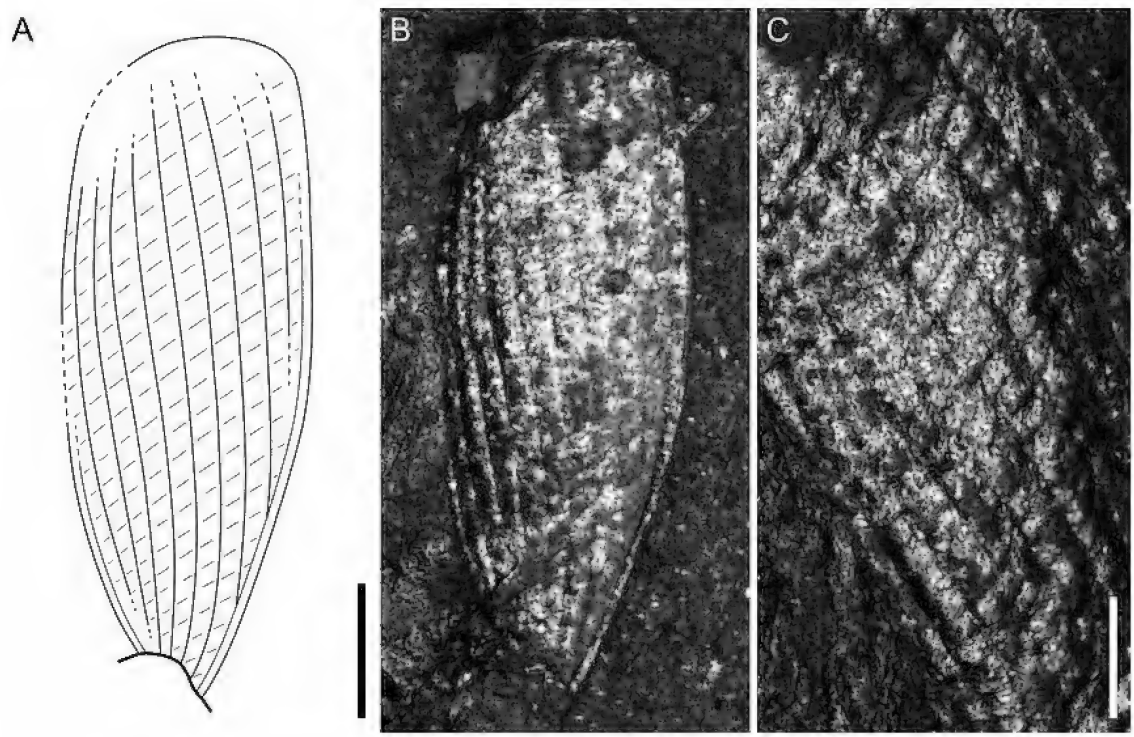

FIG. 79. Striate elytral morphotype 98, VMNH 97590. Photographs taken without ethanol. Scale bars: A, B: 0.5 mm; C: 0.25 mm.

Morphotype 98

Figure 79A–C

DESCRIPTION: Isolated elytron (no counterpart) from the Walnut Cove Formation. Small (2.5 mm long, 1 mm wide), striate; preservation good, convex in relief. Asymmetrical, narrow, length 2.5× width, width subequal in basal half, tapering apically. Basal and lateral margins convex; corners obtuse, rounded; apex obscured by matrix. Lateral rim thin, distinct. Nine striae, raised, not parallel to lateral margins, converging apically; forming squarish cells separated by depressed crossveins.

MATERIAL: Single specimen, VMNH 97590.

COMMENTS: The long veins and squared cells of this specimen resemble the elytra of Archostemata. Specimen has a similar texture to elytra of Cow Branch morphotype 54 (fig. 59) and Walnut Cove specimen VMNH 97551 (3.2 mm long, 1.3 mm wide).

DISCUSSION

Solite Entomofauna

The Solite insect collections, consisting of about 9400 specimens in total, contain insects from both the Cow Branch and Walnut Cove formations. Approximately 8100 insect fossils have been collected from the Cow Branch Formation to date, 60% of which are identifiable to order. Of these, Hemiptera make up the vast majority of specimens (78%; table 3); within Hemiptera, 94% of the specimens belong to Nepomorpha (Heteroptera), ~5% to Sternorrhyncha, and ~1% are unidentified to suborder. Beetles are the second most abundant group, but they only comprise 10% of specimens from the Cow Branch. Often uncommon in Triassic

TABLE 3

Composition of Solite Insect Fauna

Percentages of each insect order collected from the Cow Branch and Walnut Cove formations.

Order	Cow Branch (%)	Walnut Cove (%)	Total % (Walnut Cove + Cow Branch)
Blattodea	<1	7	1
Coleoptera	10	87	19
Diptera	8	<1	7
Hemiptera	78	1	69
Orthoptera	1	4	2
Thysanoptera	1	0	1
Other	1	<1	1

deposits, Diptera are surprisingly abundant and diverse here, comprising 8% of specimens, with 8 families, 11 genera, and 16 species (Blagoderov et al., 2007). Interestingly, even though Diptera are more delicate than the beetles, appendages of the fossil flies in this deposit are frequently preserved.

In contrast to the Cow Branch Formation, the insects of the Walnut Cove Formation are poorly studied and have not been systematically excavated. Only about 1300 insects have been recovered from this formation to date, 52% of which are identifiable to order. Of these, the vast majority (87%) are beetle remains, mostly isolated elytra. Fragments of roaches (7%) and orthopterans (4%) are the only other appreciable groups preserved here. Interestingly, no aquatic insects (e.g., Nepomorpha) are known from this site.

The insect faunas of these two formations differ remarkably (table 3), most notably in the overwhelming abundance of Hemiptera in the Cow Branch Formation, compared with a single plausible hemipteran (a sternorrhynchan, VMNH 97189) from the Walnut Cove Formation. Heteroptera is totally absent in the Walnut Cove strata, but this might be expected given the restricted stratigraphic distribution of Heteroptera in the Cow Branch Formation combined with the lack of stratigraphic sampling of the Walnut Cove. It is also important to note that the Cow Branch and Walnut Cove formations are separated in time by at least a few million years. Therefore, some of the faunal differences between the two sites can probably be explained by changing paleoenvironmental conditions such as ecological succession over that duration. Moreover, changes in lake depth, and thus pressure, caused by climatic shifts related to orbital forcing would have played a role in the quality of fossil preservation at each site. Olsen et al. (2015) discussed the lack of microlaminations in the older Walnut Cove strata, likely caused by a higher energy environment with sedimentary rippling in which water currents could reach the lake bottom. A shallow, wind-mixed environment would also explain the high degree of disarticulation as well as the lack of delicate, softer-bodied insects like thrips, flies, and sternorrhynchans in the Walnut Cove material.

Solite Beetles

Beetles are fairly abundant in the Solite deposit, making up 19% of identifiable insect specimens. Due to their two-dimensional, and often dorsal preservation, taxonomic assignment beyond order

is not possible for the vast majority of the Solite beetles. Of the 100 morphotypes discussed herein, there are only a few in which tentative assignments can be made. Most beetles in suborder Archostemata possess distinct elytral "window punctures." Beetles that have similar rows of large, squarish punctures (but without the thin cuticular "windows") include the unrelated and putatively much more recent elateriform family Lycidae, as well as various cucujiform families (e.g., Cryptophagidae, Cerylonidae, Colydiidae, among others). Though squarish punctures alone are not diagnostic for Archostemata, structure of the punctures in the Solite fossils is most consistent with this suborder. Two elytral morphotypes (72 and 73; fig. 71) possess these distinct elytral punctures and can therefore be considered as archostematans. Phoroschizidae (= Schizophoridae; Bouchard and Bosquet, 2020) is another taxon possibly identifiable in the Solite deposit, with morphotypes 5, 24, and 25 (figs. 7, 27, 28) potential members based on general body proportions. This extinct family (Permian to Early Cretaceous) is the only presumed aquatic member of suborder Archostemata, having adaptations for living underwater (e.g., processes or "schiza" on the elytra that connected them to the abdomen's outer edges to create an underwater "airlock") but no adaptations for swimming, such as tibial and tarsal fringes (Ponomarenko, 2003). Unfortunately, schiza are only visible on a single Solite specimen, elytron morphotype 75 (fig. 72D–F).

Several other Solite morphotypes appear to be aquatic. Morphotypes 9, 34, and 35 (figs. 11, 39, 40) have streamlined bodies somewhat resembling those of modern aquatic beetles (e.g., Dytiscidae, Gyrinidae, Haliplidae). One morphotype (13; fig. 15) also has a very faint fringe of setae on its hind leg, which might have functioned as a swimming fringe. Additionally, several specimens (e.g., VMNH 97986, figs. 37, 38) have been placed in the extinct, aquatic beetle family Coptoclavidae (*Holcoptera solitensis*; suborder Adephaga: Dytiscoidea) due to their distinct elytral markings. One particular unit of the Cow Branch Formation in quarry pit C has yielded a number of larval specimens (fig. 80) referred to form genus *Mormolucoides* (Huber et al., 2003; Fraser et al., 2017). The poor preservation in all deposits where *Mormolucoides* is preserved prevents a definitive classification, but Huber et al. (2003) suggested that the retracted head, large mandibles, and U-shaped frontal suture preserved in Early Jurassic specimens suggest a coleopteran affinity. Moreover, the units of the Cow Branch Formation (as well as those of other Newark Basin deposits) that preserve abundant *Mormolucoides* are the same units from which isolated *Holcoptera* elytra are known. This has led Huber et al. (2003) to speculate that *Mormolucoides* might be the juvenile form of *Holcoptera*. While the Solite "*Mormolucoides*" has an apparent head capsule, it unfortunately possesses few to no morphological details (e.g., mouthpart, antennal, and leg structure, or urogomphi, etc.) that can confirm placement within Coleoptera.

The lack of obvious aquatic traits (e.g., fusiform bodies, paddle-shaped legs, setal fringes) as well as the abundance of structures inconsistent with an aquatic lifestyle (e.g., elytral punctation, nodules, setation) in the remaining Solite morphotypes indicate that many of these beetles were terrestrial or littoral, living on or near vegetation surrounding the ancient lake, like the Orthoptera, Sternorrhyncha, and Thysanoptera known from this deposit. A few morphotypes even show morphologic similarities to established terrestrial taxa. One Solite beetle with a possible terrestrial lifestyle is *Leehermania prorova* (Chatzimanolis et al., 2012), which was assigned to the family Staphylinidae (suborder Polyphaga) due to its truncated elytra (fig. 19). However, this assignment was later challenged by Fikáček et al. (2020), with a proposed hydroscaphid affinity (suborder Myxophaga) for the genus. Today, members of Hydroscaphidae are aquatic, bringing *Leehermania*'s habitat back into question. Moreover, a myxophagan species with excellent, three-dimensional preservation was described from a Triassic coprolite, putatively belonging to a dinosauriform (Qvarnström et al.,

FIG. 80. Possible beetle larvae, "*Mormolucoides*." **A.** VMNH 95392. **B.** VMNH 96758. Scale bars: 1 mm.

2021). The various states of disarticulation of these beetles indicate that they were not consumed intentionally, but rather ingested along with algae. A second Solite beetle, morphotype 17 (fig. 20), shares a similar habitus and may share an affinity with *Leehermania*.

There are also two Solite specimens that, at least superficially, resemble weevils (superfamily Curculionoidea). Morphotype 57 (fig. 62) shares a similar habitus to the family Obrieniidae (Zherikhin and Gratshev, 1993), a controversial family originally assigned to Curculionoidea, but more recently suggested to belong to Archostemata (Gratshev and Zherikhin, 2003). This group is known from the Middle to Late Triassic Madygen Formation and the Late Jurassic Karatau Formation. This Solite morphotype most resembles the Jurassic species *Kararhynchus occiduus* (Zherikhin and Gratshev, 1993; Legalov, 2012) because of its short, broad rostrum. However, the Solite specimen's larger size and filiform antennae lacking an apical club differ from published obrieniids. A second Solite specimen, morphotype 58 (fig. 63) shares several traits similar to, though not taxonomically diagnostic of, modern weevils: an expanded preocular area, convex elytra with rows of punctures, and swollen femora. However, due to a lack of preserved

diagnostic features, this specimen cannot be confirmed as an early weevil despite the striking outward resemblance.

On a much broader scale, an interesting pattern was observed in the elytral shape of the Solite beetles. In the elytra of almost all modern beetles, the sutural margins are straight where the two elytra meet medially (as in, e.g., morphotype 35, fig. 40). Interestingly, 33 of the Solite beetle morphotypes have elytra in which both margins are convex such that distinguishing which is the sutural margin can be difficult (e.g., morphotypes 5, 47, and 54; figs. 7, 52, 59). Moreover, the proportion of elytra with convex versus straight margins differs significantly between the two formations of the Solite deposit. In the younger Cow Branch Formation (which contains mostly articulated morphotypes), 71% of morphotypes with visible elytral margins are straight, while 29% are convex. The opposite is true for the slightly older Walnut Cove Formation (which contains only isolated elytral morphotypes): 31% of morphotypes with visible margins are straight, whereas 69% are convex. While convex elytral margins could potentially be a taphonomic phenomenon caused by compression during the fossilization process, many of the Walnut Cove morphotypes are preserved in relief, indicating that they underwent little to no distortion (e.g., morphotype 64, fig. 68E, F). Moreover, this trait is exhibited by other Mesozoic beetles (e.g., species in Dunstan, 1923; Ponomarenko, 1969; Whalley, 1985; Arnol'di et al., 1991), suggesting that perhaps straight sutural margins did not become ubiquitous until later in the evolutionary history of Coleoptera.

Modern Faunal Comparisons

Notably, the distribution of body sizes in the Solite beetle fauna closely matches that of modern beetle communities. The articulated Solite beetles range from 1.6 mm to 12.7 mm in total length (fig. 81), with a single outlier of >33 mm. Of the 58 articulated Solite morphotypes in which length is measurable, 30 (52%) fall in the range of 2 to 4 mm. Interestingly, this size range is also known to be the most common in some modern beetle faunas. An examination of body length in the Coleoptera of Britain found that this same range of 2–4 mm was the most prevalent size class (May, 1978). A second study of beetles in a Bornean rainforest found that a similar range, between 2 and 3 mm in length, was the most common in their samples (Morse et al., 1998). Perhaps this similarity in body-size distributions between the Triassic and modern beetles, separated in time by ~220 million years, reflects the initial stages of modernization of Order Coleoptera.

A second remarkable finding is that very few of the Solite beetle specimens appear to be conspecific (if so, it was noted in the morphotype accounts). While some of the articulated morphotypes (14%) have a few (2–4) probable members, the majority (83%) are represented by a single specimen, and only two "morphotypes" (*Leehermania,* 51 specimens; *Holcoptera*, 26 specimens) are somewhat abundant. Comparing isolated elytron specimens to each other is more difficult because of their generally poorer preservation and fewer diagnostic characters, but the same species abundance distribution pattern seems to hold here as well. Only a small number of elytral morphotypes (16%) seem to have more than one possible member; the majority of morphotypes (84%) are based on one specimen, and only a single morphotype (82; fig. 76E, F) is somewhat common with 10 possible members of similar size and proportions.

This pattern somewhat follows the species abundance distribution of modern animal communities, in which a community is comprised of many rare species and only a few common species. For example, in the study of Bornean rainforest beetles, 58% of the total 859 species were represented by one individual each (Morse et al., 1988). In another study of rainforest beetles in northern Australia, 40% of species were represented by a single specimen (Monteith and Davies, 1984), and in a third study examining the arboreal insect community of an Australian

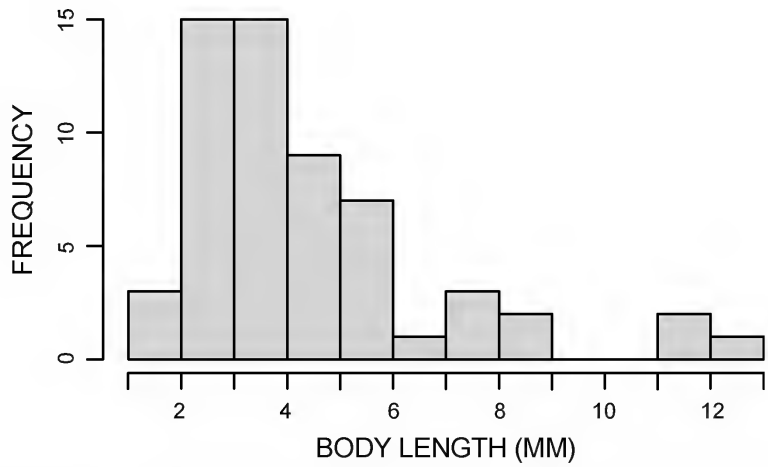

FIG. 81. Histogram of beetle body lengths for articulated morphotypes in which total length was measurable. The very large morphotype measuring >33 mm (morphotype 61) is omitted.

rainforest tree collected over a two-year period, only a single individual was collected for 34.4% of beetle species (Basset and Kitching, 1991). While high, these percentages are still quite a bit lower than the 81% of Solite beetle morphotypes (elytral + articulated) known from a single specimen. Perhaps contributing to a widespread lack of conspecifics in the Solite material is the sporadic nature of the fossilization process, as well as the poor preservation of many specimens. Within the Cow Branch material alone, 40% of specimens were not identifiable to order, and many of the identifiable specimens were too poorly preserved for recognition beyond order. Better preservation of more specimens would likely lead to the recognition of at least a few additional conspecifics, but the prevalence of rare taxa is unmistakable.

Two taxa, *Holcoptera* and *Leehermania,* are somewhat abundant in the Solite deposit, likely owing to their aquatic and possibly littoral habitats. Together, they comprise 7% (77/1080) of the Solite beetles, but they by no means dominate the fauna. In all modern ecosystems, a few very common species comprise a high percentage of the individual organisms in a fauna (McGill et al., 2007), so why is this ubiquitous pattern not apparent at Solite? Where are the very common beetle species? Perhaps this apparent lack of common beetles is due to a taphonomic bias, one possibility being size sorting. If the most common Solite beetles were exceptionally small, perhaps they were either not preserved, or their fossils were overlooked during collecting. This seems unlikely however, as very small beetles and other insects (thrips, hemipterans, etc.) are fairly abundant in the Solite collections. Alternatively, perhaps the common beetle species were quite large. Large insects are poorly represented in the Solite collections with only four of the articulated beetles reaching body lengths greater than 10 mm. This notion, however, is contradicted by the dominance of small body size (2–4 mm) in modern beetle communities discussed above, a phenomenon that is apparently mirrored by the Solite fauna. Given this, the dominance of large beetle species would not be expected at Solite. A third possibility is that the common beetle species living around ancient lake Solite had lifestyles or morphological traits that prevented their preservation in the ancient lake. If the dominant beetles were, for example, wood-boring, burrowing, or living in dung, they would be far less likely to become trapped in the ancient lake, making the few (if any) individuals that did fossilize appear to be rare. Or, perhaps some aspect of their morphology affected their postmortem buoyancy, thereby precluding pres-

ervation. For example, beetles with profuse pilosity would likely be more buoyant, preventing them from sinking to the lakebed.

Together, these two notable observations of the Solite beetle fauna provide a puzzling picture of its paleoentomofauna. The body-size distribution, which so closely matches that of modern beetle communities, reflects a lack of taphonomic size sorting in the Solite material. This suggests that the Solite deposit preserves a truly autochthonous paleofauna. Conversely, however, the exceptional proportion of unique morphotypes indicates the presence of some other taphonomic bias that prevented the preservation of the most common beetle species. These two factors together demonstrate the uniqueness of the Solite fauna and its importance in understanding coleopteran diversity during the Late Triassic.

Early Mesozoic Faunal Comparisons

Beetles have been reported from over 50 Triassic localities worldwide, spanning every continent (table 4). The Anisian (early Middle Triassic) Voltzia Sandstone of France is the earliest Triassic deposit preserving diverse Coleoptera; though isolated elytra only make up 11% of the insect specimens there, beetles are the most diverse group (Papier et al., 2005). Insect-bearing deposits increase in abundance during the Carnian (early Late Triassic), with three of the most prolific formed during this stage. In the Molteno Formation of South Africa, beetles comprise roughly 22% of insect specimens, second only to roaches. However, the beetles are the most diverse insect order at this site, with roughly half the species reported to belong to Coleoptera (Cairncross et al., 1995). In the Los Rastros Formation of Argentina, beetle elytra, hemipteran forewings, and blattodean tegmina—all sclerotized structures—are the most common fossils present, though the authors do not provide numerical data on the abundance of each group (Mancuso et al., 2007). The Madygen Formation (Ladinian-Carnian) of Kyrgyzstan is the richest Triassic insect locality in the world and its fauna is dominated by beetles (mostly isolated elytra), which make up roughly 23% of the 15,000 individual insects collected. Beetles are an even larger component of the Norian (middle Late Triassic) Denmark Hill insect bed (Blackstone Formation) of Queensland, Australia, where they comprise roughly 50% of collected specimens (Tillyard and Dunstan, 1924: table C); the majority of the remaining insects belong to "Homoptera" (e.g., Auchenorrhyncha), Blattodea, and Heteroptera (Tillyard and Dunstan, 1924).

Also Norian in age (Olsen et al., 2015), the Solite deposit is dominated by Heteroptera (predominantly Nepomorpha) and Coleoptera (table 3). Roaches are notably scarce (1%) here, in stark contrast to their proportion at the other major Triassic sites (e.g., Madygen Formation [>25%], Molteno Formation [46%], Denmark Hill insect bed [13%]). Beetles are the second most abundant group, comprising roughly 19% of identifiable insect specimens, a similar percentage to those of the Molteno (22%) and the Madygen (23%) formations. From Solite, 100 morphotypes have been sorted from the roughly 1000 beetle specimens recovered (table 5). This is a higher diversity of beetles than reported for the Voltzia Sandstone from which 32 morphotypes were recorded from 584 specimens. This is only about one-third the number of morphotypes from half the number of individuals as compared to Solite, but this lower diversity might be expected given the older age of the Voltzia Sandstone. A much higher level of beetle diversity than that of both Solite and the Voltzia Sandstone has been reported from the Molteno Formation, with 161 morphotypes sorted from only 453 beetle specimens. This is roughly 1.5× the diversity of Solite reported from fewer than half the number of specimens. However, given the fragmentary preservation of the Molteno insects (Anderson et al., 1998), this number of morphotypes is likely an overestimate. Conversely, only about 73 species have been described from the roughly 3500 beetle specimens of the Madygen Formation (Ponomarenko, 1969; Arnol'di et al., 1991; Ponoma-

TABLE 4

Beetles of the Triassic Period

List of Triassic deposits from which beetle fossils are known.

Age	Location	Deposit/Formation	References
Late Permian/ Early Triassic	Siberia, Russia	Mal'tsevo Fm.	Ponomarenko and Volkov, 2013; Volkov, 2013
Late Permian/ Early Triassic	Madhya Pradesh, India	Parsora Fm.	Ghosh et al., 2007
Late Permian/ Early Triassic	Yug River and Vologda Regions, Russia	Vokhmian Fm.	Lozovsky et al., 2016; Ponomarenko, 2004, 2016b
Early Triassic	Queensland, Australia	Arcadia Fm.	Northwood, 2005
Olenekian	Yaroslavl Region, Russia	Rybinsk Fm.	Ponomarenko, 2004, 2016b
Olenekian/ Anisian	Nenets National District, Russia	Nyadeita Fm.	Ponomarenko, 2008
Olenekian/ Ladinian	Germany	Röt Fm. (Buntsandstein)	Bashkuev et al., 2012; Brauckmann and Schluter, 1993; Ponomarenko et al., 2015; Ponomarenko and Bashkuev, 2018
Anisian	France	Grès à Voltzia	Papier et al., 2005
Anisian	The Netherlands	Vossenveld Fm.	van Eldijk et al., 2017
Anisian	New South Wales, Australia	Ashfield Shales Fm.	Tillyard, 1918
Ladinian	Spain	"Pedra d'Alcover"	Via and Calzada, 1987
Ladinian	San Juan Province, Argentina	Casa de Piedra Fm.	Hauschke, 1991
Ladinian	Switzerland	Meride Limestone	Krzeminski and Lombardo, 2001; Strada et al., 2014
Ladinian	France	Muschelkalk	Fliche, 1901
Ladinian	Shaanxi Province, China	Yanchang Fm. = Tongchuan Fm.	Hong, 1980, 1984; Liu et al., 1985; Zheng et al., 2018
Ladinian/ Carnian	La Rioja Province, Argentina	Ischichuca Fm.	Martins-Neto and Gallego, 2009
Ladinian/ Carnian	Germany, Liechtenstein, Spain, Switzerland	Keuper	Fedorenko, 2014; Geyer and Kelber, 1987; Heer, 1853, 1877; Peñalver et al., 1999; Ponomarenko et al., 2015; Prokin et al., 2013; Zeuner, 1930
Carnian	Mendoza Province, Argentina	Cacheuta Fm.	Martins-Neto et al., 2006
Carnian	Xinjiang, China	Huangshanjie Fm.	Lin, 1992
Carnian	Mendoza Province, Argentina	Ischigualasto Fm.	Frenguelli, 1948
Carnian	Kazakhstan	Koldzat Fm.	Ponomarenko, 1969
Carnian	Poland	Krasiejów strata	Dzik and Sulej, 2007; Qvarnström et al., 2021
Carnian	La Rioja Province, Argentina	Los Rastros Fm.	Gallego, 1997; Martins-Neto et al., 2006
Carnian	Austria	Lunz Fm.	Meller et al., 2011
Carnian	Kyrgyzstan	Madygen Fm.	Arnol'di et al., 1991; Ponomarenko, 1967, 1969; Yan et al., 2017a, 2017b; Zherikhin and Gratshev, 1993

TABLE 4 *continued*

Age	Location	Deposit/Formation	References
Carnian	South Africa	Molteno Fm.	Anderson et al., 1998; Riek, 1974, 1976; Zeuner, 1960
Carnian	Japan	Momonoki Fm.	Fujiyama, 1973; Maeda and Oyama, 2019
Carnian	Virginia/Maryland	Newark Supergroup, Taylorsville Basin: Doswell Fm.	Cornet and Olsen, 1990
Carnian	Mendoza Province, Argentina	Potrerillos Fm.	Lara et al., 2012; Martins-Neto et al., 2007, 2008
Carnian	Southern-central Chile	Santa Juana Fm.	Gallego et al., 2005
Carnian	South Region, Brazil	Santa Maria Fm.	Pinto and Ornellas, 1974
Norian	Primorye District, Russia	Amba Fm.	Zherikhin and Gratshev, 1993
Norian	Germany	Arnstadt Fm.	Zeuner, 1930
Norian	Queensland, Australia	Blackstone and Mount Crosby Fms., Ipswich Coal Measures	Dunstan, 1923; Riek, 1970; Tillyard and Dunstan, 1916
Norian	Virginia	Newark Supergroup, Culpeper Basin	Gore, 1988
Norian	Virginia and North Carolina	Newark Supergroup, Dan River Basin: Cow Branch Fm.	Chatzimanolis et al., 2012; Fraser et al., 1996; Fraser and Grimaldi, 2003; Huber et al., 2003; Thomson et al., 2017
Norian	North Carolina	Newark Supergroup, Durham Subbasin	Olsen and Huber, 1997
Norian	Ukraine	Protopivka Fm.	Arnol'di et al., 1991
Norian	East Kazakhstan	Tologoi Fm.	Arnol'di et al., 1991; Ponomarenko, 1969, 1993; Zherikhin and Gratshev, 1993
Norian	Hunan Province, China	Zijiachong Fm.	Lin, 1986
Rhaetian	Italy	Argilliti di Riva di Solto Fm.	Whalley, 1986
Rhaetian	Turkey	Çakrazboz Fm.	Laurentiaux, 1946
Rhaetian	England	Cotham Fm.	Giebel, 1856; Handlirsch, 1906–1908
Rhaetian	Sweden	Höganäs Fm.	Heer, 1878
Rhaetian	Sukhomesovo, Russia	Korkino Fm.	Martynov, 1935
Rhaetian	England	Lilstock Fm.	Brodie, 1845; Cockerell, 1915; Giebel, 1856; Thomson et al., 2017
Rhaetian	Hunan Province, China	Sanqiutang Fm.	Lin, 1983, 1986
Rhaetian	Germany	Unknown	Handlirsch, 1906–1908; Roemer, 1876; Zeuner, 1930
Rhaetian	Auckland, New Zealand	Unknown	Grant-Mackie, 1958
Late Triassic	Angola	Camadas com peixes Fm.	Teixeira, 1975
Late Triassic	Xinjiang, China	Haojiagou section	Zhang et al., 2022
Late Triassic	Anhui, Eastern China	Lalijian Fm.	Huang, 1984; Zhang et al., 2022
Late Triassic	Hebei Province, Eastern China	Laohugou Fm.	Huang et al., 2019

TABLE 4 *continued*

Age	Location	Deposit/Formation	References
Late Triassic	Mendoza Province, Argentina	Llantenes Fm.	Brauckmann et al., 2010
Late Triassic	Guangdong, China	Xiaoping Fm.	Lin and Mou, 1989
Late Triassic	Xinjiang, China	Xiaoquangou Group	Guan et al., 1998; Zhang et al., 2022
Late Triassic	Victoria Land, Antarctica	Section Peak Fm.	Bomfleur et al., 2011
Late Triassic/ Early Jurassic	England	Lias Group	Brodie, 1845; Cockerell, 1915; Crowson, 1962; Gardiner, 1961; Giebel, 1856; Handlirsch, 1906–1908; Thomson et al., 2017

renko, 1995; 2002), though this too is likely misleading. Shcherbakov (2008) noted that much of the Madygen material remains unstudied and that the 73 described species are only a fraction of the diversity preserved there.

Faunal Turnover and Paleobiogeography

It is important to note both the rapidity with which beetles diversified during the Triassic to become dominant members of the entomofauna, as well as the magnitude of the turnover in taxa between the Permian and the Late Triassic. During the late Permian, the diversity of Coleoptera remained low; the order was represented by only a few early stem groups (Permocupedidae, Rhombocolediae, and Asiocoleidae), as well as the earliest members of suborder Archostemata. During this period, beetles were uncommon in insect assemblages (1%–3%; Ponomarenko, 2002).

The End Permian Mass Extinction (EPME) event marked a dramatic faunal turnover in the Coleoptera, with the majority of Permian taxa becoming extinct near the boundary. Not only did beetles subsequently diversify and become a major component of the fauna, but the composition of taxa changed dramatically into the Triassic, becoming dominated by new groups including Cupedidae and Phoroschizidae (suborder Archostemata; Zhao et al., 2021). By the time the Cow Branch and Walnut Cove formations were deposited, only ~30 million years after the EPME (a relatively short period of geologic time), the composition of the entire beetle fauna had changed from the primitive "protobeetles" of the Permian to early members of the extant suborders (and possibly even some extant families).

To put 30 million years after the EPME into perspective, consider the evolutionary history of Cenozoic beetles. For example, beetles are abundant in Baltic amber, which is estimated to be roughly 44 million years old (Ritzkowski, 1997). In the span of time between the formation of Baltic amber and today (~14 million years longer than the duration between the EPME and the deposition of the Solite deposit), beetles have changed remarkably little: of the 287 known beetle genera preserved in Baltic amber, almost half (48%) are extant, and only a single beetle family (of 90 total) is extinct (Alekseev, 2013). An even more striking example is the archostematan beetle, *Micromalthus debilis*. *M. debilis* is an extant species that is also known from 15 to 20 million-year-old Dominican amber (Hörnschemeyer et al., 2010), demonstrating that a single insect species can morphologically persist at least 15 million years. Using these Cenozoic intervals as a metric for beetle evolution, the faunal turnover in the ~30 million years following the EPME saw profound and rapid radiation, not only in the dominant genera or families, but also in the dominant suborders of beetles.

Not only did the coleopteran fauna change dramatically from the Permian into the Triassic, but the composition of beetle taxa also differs among Triassic deposits of similar age. Even at the higher taxonomic levels, the Norian Solite assemblage (ca. 220 Ma; Olsen et al., 2015; Kent

TABLE 5

Abundance of Beetles in the Major Triassic Deposits

Comparison of the numbers of insect specimens, beetle specimens, and beetle morphotypes known from the major Triassic insect deposits.

Age	Location	Deposit	Insect Specimens (no.)	Beetle Specimens (no.)	Beetles (%)	Beetle Morphotypes/ Species (no.)	Reference
Anisian	France	Voltzia Sandstone	5300	584	11	32	Papier et al., 2005
Carnian	South Africa	Molteno Fm.	2056	453	22	161	Cairncross et al., 1995
Ladinian-Carnian	Kyrgyzstan	Madygen Fm.	15,000	3500	23	73+	Shcherbakov, 2008
Norian	Australia	Denmark Hill insect bed	Not Reported	Not Reported	50	58	Tillyard and Dunstan, 1924
Norian	Virginia and North Carolina	Solite Deposit:					this study
		Cow Branch Fm.	4885	501	10	71	
		Walnut Cove Fm.	667	580	87	29	
		Total	5552	1083	19	100	

et al., 2017) differs significantly from those of other deposits. This is perhaps most apparent in the proportion of Archostemata, a suborder that is present at Solite, but in a much smaller proportion than elsewhere. For example, archostematans comprise about 90% of beetles from the Madygen Formation (Ladinian-Carnian; Shcherbakov, 2008), they are reported to make up the majority of Triassic beetles from China (Middle-Late Triassic; Zhang et al., 2022), and are also the dominant beetle taxon present in the Los Rastros Formation of Argentina (Carnian; Mancuso et al., 2007). In contrast, very few Solite morphotypes can confidently be placed in this suborder. Note, however, that many authors assign isolated elytron specimens to Archostemata, possibly contributing to the high proportion of this suborder in other Triassic deposits.

Shared taxa between the Solite deposit and other Triassic deposits are also quite rare. A thorough analysis of the Solite beetle fauna has produced only a few examples of morphotypes also known from other Triassic sites, but some striking similarities exist in Jurassic Eurasian deposits, specifically from the Early Jurassic Lias Group of the United Kingdom. In addition to Coleoptera, this has also been noted in Orthoptera (Elcanidae), Mecopterida (Pseudopolycentropodidae), and Amphiesmenoptera (Necrotauliidae), a pattern that can be explained by the continental configuration of the Mesozoic (Pierwola and Grimaldi, 2022).

While a few Solite beetles show some degree of morphological similarity to specimens from other Triassic localities (as discussed in the description of each morphotype), only a single definitive shared taxon is known. This morphotype was formerly assigned to the genus *Holcoptera*, a member of the extinct, aquatic beetle family Coptoclavidae, which is known from a few Rhaetian (latest Late Triassic) sites in England. The Solite specimens were described as *Holcoptera solitensis* (figs. 37, 38) based on two isolated elytra (Thomson et al., 2017); since the species' original description, a few, less fragmentary specimens have been identified. A total of 26 holcopteran specimens are currently known from the Solite material, seven of which consist of

TABLE 6

Beetles of the Jurassic Period

List of selected Jurassic deposits from which beetle fossils are known.

Age	Location	Deposit/Formation	Selected References
Late Triassic/ Early Jurassic	Dorset, England	Lower Lias	Brodie, 1845; Ponomarenko, 2006; Whalley, 1985; Zeuner, 1962
Early Jurassic	Liaoning and Hebei, China	Beipiao Fm.	Chang, 1996; Hong, 1998
Early Jurassic	Hubei, China	Wuchang Fm.	Tan and Ren, 2009 (and references therein)
Early Jurassic	Xinjiang, China	Badaowan Fm.	Zhang, 1997
Early Jurassic	Connecticut	Portland Fm.	Huber et al., 2003
Early Jurassic	Massachusetts	Mount Toby Fm.	Huber et al., 2003
Early Jurassic	New Jersey	Towaco Fm.	Huber et al., 2003
Early Jurassic	Andhra Pradesh, India	Kota Fm.	Rao and Shah, 1959 (and references therein)
Early Jurassic	Batken Region, Kyrgyzstan	Sulyukta Fm.	Arnol'di et al., 1991 (and references therein); Ponomarenko, 1969
Early Jurassic	Tong Region, Kyrgyzstan	Dzhil Fm. (Issyk-Kul Site)	Arnol'di et al., 1991 (and references therein); Ponomarenko, 1969
Early Jurassic	Osh Region, Kyrgyzstan	Kyzyl-Kiya Locality	Ponomarenko, 1969
Early Jurassic	Victoria Land, Antarctica	Shafer Peak Fm.	Bomfleur et al., 2011
Early Jurassic	Western Australia	Cattamarra Coal Measures (Mintaja Insect Locality)	Martin, 2010; Riek, 1968
Hettangian-Sinemurian	Poland	Zagaje Fm.	Wegierek and Zherikhin, 1997
Toarcian	North Germany	"Green Series"	Ansorge, 1996, 2003; Handlirsch, 1906–1908
Toarcian	Germany	Posidonia Shale	Ansorge, 2003; Bode, 1953; Brachert, 1987; Ponomarenko, 1992
Early/Middle Jurassic	Osh Region, Kyrgyzstan	Sai-Sagul Locality	Sukacheva and Rasnitsyn, 2004
Middle Jurassic	Oxfordshire, England	Taunton Limestone Fm.	Ponomarenko, 2006; Westwood, 1854
Middle Jurassic	Inner Mongolia and Hebei, China	Jiulongshan Fm.	Bai et al., 2012; Cai et al., 2012; Chang et al., 2009; Hong, 1998; Hsiao et al., 2017; Liu et al., 2017; Pan et al., 2011; Tan and Ren, 2009
Middle Jurassic	Guangxi, China	Shiti Fm.	Li et al., 2021
Middle Jurassic	Hebei, China	Xiahuayuan Fm.	Tan and Ren, 2009 (and references therein)
Middle Jurassic	Jiangxi, China	Dameigou Fm.	Tan and Ren, 2009 (and references therein)
Middle Jurassic	Xinjiang, China	Xishanyao Fm.	Zhang, 1997
Middle Jurassic	Transbaikal, Russia	Ichetui Fm.	Arnol'di et al., 1991 (and references therein)

TABLE 6 *continued*

Age	Location	Deposit/Formation	Selected References
Middle Jurassic	Irkutsk, Russia	Cheremkhovo Fm.	Arnol'di et al., 1991 (and references therein)
? Middle Jurassic	Western Antarctica	Mount Flora Shales	Carpenter, 1969; Tasch, 1973; Zeuner, 1959
Callovian	Wyoming and Montana	Sundance Fm.	Santiago-Blay et al., 2001
Middle/Late Jurassic	Inner Mongolia, China	Daohugou Fm.	Wang and Zhang, 2011; Wang et al., 2010; Yan and Wang, 2010; Yan et al., 2014
Middle/Late Jurassic	Karatau, Kazakhstan	Karabastau Fm.	Arnol'di et al., 1991 (and references therein); Legalov, 2010, 2012; Ponomarenko, 1969; Rodendorf, 1968
Middle/Late Jurassic	Transbaikal, Russia	Uda Fm.	Arnol'di et al., 1991 (and references therein)
Middle/Late Jurassic	Santa Cruz Province, Argentina	La Matilde Fm.	Lara et al., 2012; Martins-Neto and Gallego, 1999
Middle/Late Jurassic	Western Mongolia	Togo-Khuduk Sequence (Bakhar Locality)	Ponomarenko, 1994, 1997
Late Jurassic	Southwestern Mongolia	Shar Teg Sequence	Ponomarenko et al., 2014
Late Jurassic	Jilin, China	Baojiatun Fm.	Tan and Ren, 2009 (and references therein)
Late Jurassic	Gansu, China	Chijinqiao Fm.	Tan and Ren, 2009 (and references therein)
Late Jurassic	Bavaria, Germany	Solnhofen Limestone	Barthel et al., 1990; Carpenter, 1932; Ponomarenko, 1985
Late Jurassic	Central Mongolia	Ulan-Ereg Fm.	Ponomarenko, 1997
Kimmeridgian-Tithonian	New South Wales, Australia	Talbragar Fish Bed	Ashman et al., 2015; Beattie and Avery, 2012; Cai et al., 2013; Oberprieler et al., 2016

more than a single elytron. A few possess both elytra and some underlying abdominal structures, and one specimen (VMNH 96762; fig. 37C) includes the head, though it is not attached to the body. Despite the addition of these less fragmentary specimens, the Solite holcopterans do not possess any preserved diagnostic features (e.g., dorsal and ventral eyes, coxae, sternites) to support their taxonomic assignment to this genus.

While only one shared beetle taxon of Triassic age has been identified, a few other shared taxa are known from Jurassic localities (table 6). In addition to *Holcoptera*, which survived the Triassic-Jurassic boundary and has also been found in Early Jurassic strata of the eastern United States (Connecticut and Massachusetts; Huber et al., 2003) and England (several sites; Thomson et al., 2017), one additional articulated Solite morphotype shows a clear similarity to Liassic specimens of Eurasia. Solite morphotype 48 (fig. 53A–C) shares a striking resemblance in habitus, size, and elytral ornamentation to the Lower Liassic "Carabidae (?)" and "Dryopoidea (?)" specimens of Dorset, England (Whalley, 1985; fig. 53D, E). There are also two elytral morphotypes that show striking similarities to published Jurassic specimens. Morphotype 78 (fig. 74) from the Walnut Cove Formation shares a remarkable similarity to phoroschizid elytral specimens from the Upper Jurassic Shar Teg Lagerstätte of Mongolia

(Ponomarenko et al., 2014: figs. 29/3, 29/4). Solite Morphotype 72 (fig. 71A, B), also from the Walnut Cove Formation, is remarkably similar to a Jurassic specimen of *Zygadenia westraliensis* from Western Australia (Martin, 2010: fig. 2b; fig. 71C herein).

Aside from these few examples, the beetles of the Solite deposit are generally distinctive. The unusual method of preservation of the Solite material may play a role in the apparent uniqueness of the fauna; ventral morphology is rarely preserved, and the two-dimensional preservation of the specimens precludes the use of phylogenetic methods for taxonomic placement as in Fikáček et al. (2020). However, future studies using new techniques (e.g., SEM backscatter; Muscente and Xiao, 2015) are likely to be illuminating. Even despite the current lack of diagnostic features in the studied morphotypes, the Solite Lagerstätte preserves a remarkable diversity of beetles, providing a crucial view into the evolutionary history of Coleoptera at the dawn of their radiation.

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On the cover: Diverse beetles from the Solite Deposit of Virginia and North Carolina (clockwise from top left): Morphotypes 31, 58, 17, 29, and 23.